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SEP

CONTENTS

The Distribution and Development of Enzymes in Pea Seedlings. *Helen A. Stafford* 283

New South American Umbelliferae. *Mildred E. Mathias and Lincoln Constance* 311

A Comparison of the Three-dimensional Shapes of Cork Cambium and Cork Cells in the Stem of Pelargonium hortorum Bailey (Concluded) ——— *Frank O. Wetmore* 317

The Morphology and Cytology of Lemmanea australis Atk. *John Henry Mullahy, S.J.* 333

Bibliographic Notes on Palisot de Beauvois' Prodromus. *Howard A. Crum* 338

Torreya

Book Reviews. Field Trip Reports. Notes. ———

Index to American Botanical Literature ———

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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 79, NO. 5, PP. 351–358 SEPTEMBER, 1952

THE DISTRIBUTION AND DEVELOPMENT OF ENZYMES IN PEA SEEDLINGS[1]

HELEN A. STAFFORD[2]

Besides a knowledge of the existence of specific enzymes and their intracellular localization, information concerning their distribution within the plant and during development from the seed to maturity should shed light on the possible interrelationships between these enzymes and their significance and function in differentiation and metabolism.

The few recent investigations involving such a distribution in respect to time and region are reviewed by Goddard and Meeuse (1950). Because of experimental evidence of the presence of cyanide sensitive respiration in seedlings and its frequent absence in the mature plant, some of the developmental studies have centered about the problem of possible terminal oxidases. Others have been concerned with enzymes like catalase, peroxidase, proteases and a few dehydrogenases. Most of these enzymes increase upon germination, but a few dehydrogenases and cytochrome oxidase have been reported to decrease in activity (Davison 1949). Distribution studies have involved the enzymes ascorbic oxidase, amylase, and phosphorylase. Illustrations of these will be discussed later.

In the following investigation, seedling stages were chosen as a standard for further comparisons because they are easily grown and can therefore be obtained in bulk, and because the presence of excess food reserves permit them to be dark-grown so that the enzymes can be first studied without any complications arising from photosynthesis. Peas were chosen because numerous enzymes have now been identified in this material (Goddard and Meeuse 1950, Bonner 1950), and because the intracellular localization of the five enzymes studied, cytochrome, succinic, and ascorbic oxidases, amylase and phosphorylase, has been recently demonstrated (Stafford 1951).

While this report is only a beginning of a developmental study of enzymes in peas, these particular enzymes are of further interest because they can be studied as pairs of enzymes whose ratios of activity during

[1] The cost of this work was supported in part by grants to David R. Goddard from the American Cancer Society and the National Cancer Institute of the U. S. Public Health Service.

Part of a thesis presented to the Faculty of the University of Pennsylvania in partial fulfillment of the requirements for the Degree of Doctor of Philosophy.

The author wishes to express her gratitude to Professor David R. Goddard for his advice and assistance throughout this research.

The author held the Wellesley College Fanny Bullock Workman Fellowship for the academic year 1950–1951.

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growth and differentiation into mature plants might be of greater significance than their individual activities. The pairs of enzymes in this case would be cytochrome oxidase vs. succinoxidase, cytochrome oxidase vs. ascorbic oxidase, and amylase vs. phosphorylase.

Materials and methods. Peas (*Pisum sativum* var. *gradus*) were sterilized in 7% calcium hypochlorite for one-half hour, soaked in aerated distilled water for about 20 hours at 25° C., and then were laid out on moist filter paper in glass covered trays at the same temperature in a dark room for the required number of days.

After removing the seed coats, and washing thoroughly in distilled water, 100 g. wet weight of seedlings (either with or without cotyledons or the root-shoot axis alone) were ground in a mixture of 50% ice and 50% distilled water for 1 minute in a Waring blendor run on a variac set at 60 volts. This homogenate (H) was then strained through two layers of cheese cloth and was made up to a total volume of 286 ml. in order to make a 35% homogenate (E).

The extract E was then centrifuged at low speed ($500 \times g$) for ten minutes at 4° C. yielding a residue mainly of starch that was discarded and a supernatant M. All experiments were made on this fraction. Fraction M is comparable to one of those used in the study on intracellular localization of these enzymes reported elsewhere (Stafford 1951).

Enzyme test methods. Cytochrome oxidase, succinoxidase, and ascorbic oxidase were all tested manometrically at 25° C., using duplicate Warburg vessels. Each vessel contained in a total volume of 2.2 ml. the following: 0.2 ml. of 10% KOH in the inset; substrates in the side arm were 3 mg. of hydroquinone for cytochrome oxidase, 0.025 M sodium succinate for succinoxidase, and 4 mg. acid for ascorbic oxidase; the main compartment contained 0.04 M phosphate buffer at pH 7.1 for the first two enzymes, and at 6.0 for the third; 3×10^{-5} M cytochrome *c* was added for the first two enzymes only, and 1.0 ml. of fraction M was added to each. Endogenous respiration has been subtracted.

Amylase activity was measured in terms of mg. of maltose produced per 2 ml. enzyme during a 30 minute incubation period at pH 7.4 at 25° C. Fraction M was dialyzed for 24 hours at 4° C. against 1% KCl before use as a source of amylase or phosphorylase. Incubation mixtures contained in a total volume of 5 ml.: 0.05 M trisaminomethane buffer (TAM) (pH 7.4), 10 mg. of soluble starch, and 2 ml. of fraction M. After incubation 10% trichloracetic acid (TCA) was added to stop enzymatic activity and to precipitate the protein. After centrifugation, the filtrate was neutralized and reducing sugars were determined according to Hassid (1937) with maltose as standard. The control contained the same components except that the TCA was added prior to the enzyme preparation. The color change

of the KI_3 starch test made during the course of the reaction showed that an α-amylase was involved.

Phosphorylase activity was measured in terms of μg. of phosphorus released per ml. fraction M during a 10 minute incubation period at 25° C. with glucose-l-phosphate as substrate. The inorganic phosphorus was measured on the filtrate by the method of Sumner, Chow and Bever (1950) after the protein was precipitated with 10% TCA. The determinations were made on the same dialyzed extracts used for amylase tests. Incubation mixtures contained in a total volume of 4 ml.: 0.01 M sodium fluoride (NaF), 10 mg. of soluble starch, 10 mg. of glucose-l-phosphate in 0.05 M TAM buffer at pH 7.4, and 1 ml. fraction M. Controls were identical with the test except that TCA was added prior to the enzyme. Since a large percentage of the control value was due to acid hydrolysis of the glucose-l-phosphate, care was taken to keep controls and tests in contact with the TCA the same length of time.

Enzymatic activities were linear with time and concentration of the enzyme preparation in the above tests. Actual curves showing the relationship between activity and time and ml. of fraction M are shown elsewhere (Stafford 1951).

Results. Camparison of the enzymatic activities of the root-shoot axis with that of the cotyledons. In these experiments, either equal amounts (35% homogenates) of excised cotyledons and of the root-shoot axis from the same batch of seedlings were extracted separately for comparison or only the root-shoot axis was extracted (table 1). It was necessary to use many more root-shoots than cotyledons in order to obtain comparable wet weights of the two regions. Actual measurements of the root-shoot axis are shown in table 2 under 3 day-old plants, showing that about 80% of this axis consists of root.

When the activity is expressed in terms of g. wet weight, ascorbic oxidase occurred primarily or entirely in the root-shoot axis, while the other four enzymes were either equally divided between the two regions (amylase) or were more concentrated in the cotyledons (cytochrome and succinic oxidases and phosphorylase). The relative activity varied, however, when compared on a dry weight or protein basis. Ascorbic oxidase, cytochrome oxidase, and amylase were concentrated in the root-shoot axis, while phosphorylase and succinoxidase were predominantly in the cotyledons.

While basing the activity on dry weight or protein may be questioned because the cotyledons contain more storage products than the root-shoot axis, the different enzymes did not vary the same way (table 1). Another difficulty was that cytochrome oxidase activity was less stable in the root-shoot axis than in the cotyledons.

Although endogenous respiration represented only a small fraction of

the cytochrome oxidase activity, it was important to consider in the ascorbic oxidase test of the cotyledons and succinoxidase activity of the root-shoot. As the ascorbic oxidase test activity of the cotyledons was not greater than the endogenous respiration, this enzyme may either be completely

TABLE 1. *Comparison of enzymatic activities in 35% homogenates of the cotyledons and of the root-shoot axis of 3 day-old pea seedlings. In A, cotyledons and root-shoot axis were from the same seedling batch. In B, only the root-shoot was extracted. Calculations of the percentage activity contributed by these two regions when a 35% homogenate of the intact seedling is made are shown.*

	Cotyledons	Root-shoot axis	
	A	A	B
Cytochrome oxidase			
µl. 0_2 per hr. per g. wet wt.	406	377	363
Q_{0_2}*	4.0	7.1	8.4
Q_{0_2} (P)**	21.7	71.3	70.5
% entire seedling	91	9	.....
Succinic oxidase			
µl. 0_2 per hr. per g. wet wt.	120	25.7	11.4
Q_{0_2}	1.2	0.5	0.3
Q_{0_2} (P)	6.3	4.6	2.2
% entire seedling	97	3	.....
Ascorbic oxidase			
µl. 0_2 per hr. per g. wet wt.	0	200	280
Q_{0_2}	0	3.8	6.5
Q_{0_2} (P)	0	37.7	54.5
% entire seedling	0	100	.....
Endogenous			
µl. 0_2 per hr. per g. wet wt.	74	31	.....
% entire seedling	96	4	.....
Amylase			
mg. maltose per g. wet wt.	1.74	1.73	.....
" " per mg. dry wt.	0.017	0.033	.....
" " per mg. protein	0.094	0.336	.....
% entire seedling	90	10	.....
Phosphorylase			
µg. P per g. wet wt.	157	35.7	.....
" " per mg. dry wt.	1.51	0.67	.....
" " per mg. protein	8.4	6.95	.....
% entire seedling	97	3	.....

* $Q_{0_2} = \frac{\text{µl. } 0_2/\text{hr.}}{\text{mg. dry weight}}$ ** $Q_{0_2}\ (P) = \frac{\text{µl. } 0_2/\text{hr.}}{\text{mg. protein}}$

lacking, or present in amounts too small to be measured with this technique. Subtraction of endogenous respiration can give misleading results if the presence of the added substrate inhibits this basal activity.

In the remaining experiments concerning a developmental study of these enzymes, a 35% homogenate of the intact seedling was made. Under these conditions, 90% of the wet weight of the seedlings can be attributed to the

cotyledons alone, the root-shoot material being extremely dilute in comparison with the above experiments. The percentage activity contributed by these 2 main portions of the seedling when a 35% homogenate of the intact seedling is made are shown in table 1. These calculations are based on average wet weight values showing that 90% of the wet weight of the intact seedling is due to cotyledons.

About 90 to 97% of the total activity of cytochrome oxidase, succinoxidase, amylase, and phosphorylase is due to the cotyledons. Only a few percent or none of the ascorbic oxidase activity of the intact seedling is contributed by the cotyledons because of the low concentration or complete lack of this enzyme in seedling cotyledons. This is based on the assumption that the activity is not being limited in an isolated region by a factor supplied in the whole seedling homogenate by the missing region. Most of the cytochrome oxidase and amylase activity being measured when the intact seedling (root-shoot plus cotyledons) is extracted, therefore, is due to the cotyledons alone, not because the root-shoot axis lacks these enzymes, but because the root-shoot material is too dilute for measurement (only a 3.5% homogenate).

Comparison of the enzymatic activities of 0, 3 and 6 day-old seedlings. These experiments were based on a 35% homogenate of the intact seedling (root-shoot axis plus cotyledons). For the so-called 0 day-old stage, seeds were soaked for 18 hours at 4° C. in order to use the same extraction procedure.

All enzymes studied except ascorbic oxidase were found in 0 day-old or ungerminated seeds. All five enzymes increased in activity during germination, but with varying degrees. Data giving dry weights, seedling length, and enzymatic activities expressed on a wet weight or dry weight basis are shown in table 2. Increases of activity in terms of dry weight paralleled the activities expressed on a wet weight basis. Amylase and cytochrome oxidase activity were still rapidly increasing at 6 days, while ascorbic oxidase and succinic oxidase and phosphorylase tended to fall off after 3 days.

Succinoxidase activity in the 3 and 6 day-old stages was quite variable and was frequently unable to support activity greater than 40 μl. O_2 per hour per ml. of fraction M unless the seedlings were extracted in the presence of sodium succinate. Much less variation was found in ungerminated seeds. The high values shown for 3 day-old seedlings were consistently obtained when a sodium succinate extraction was used. It appears that the rate of oxygen uptake above a certain amount was limited by some factor in the absence of the substrate during extraction. Further experiments should be carried out to check the increase in succinoxidase activity under these more stable conditions, and also to check the manometric measure-

TABLE 2. *Comparison of the enzymatic activity of 0, 3, and 6 day-old pea seedlings. Values are based on fraction M only, and represent the average of 2 separate determinations with duplicate vessels in 0 and 6 day-old peas, and 4 to 8 in 3 day-old. Dry weight values are for the non-dialyzed extracts only.*

Age of seedlings	0	3	6
Dry weight in mg. per ml. M	35.7	33.3	35.7
Seedling length in cm.	.....	4.1	14.1
Total	.....	3.4	8.5
Root	.....	0.7	5.6
Shoot			
Endogenous respiration	0	71	66
µl. O_2 per hr. per g. wet wt.			
Cytochrome oxidase	434	522	742
µl. O_2 per hr. per g. wet wt.	4.5	5.6	7.3
Q_{O_2}			
Succinoxidase	80	169	49
µl. O_2 per hr. per g. wet wt.		(49–240)	
Q_{O_2}	0.6	0.5–2.5	0.5
Ascorbic oxidase			
µl. O_2 per hr. per g. wet wt.	8.6–21.8	109	203
Q_{O_2}	0.16	1.1	2.0
Amylase			
mg. maltose per g. wet wt.	1.09	1.96	3.37
mg. maltose per g. dry wt.	0.013	0.021	0.036
Phosphorylase			
µg. P per g. wet wt.	60.6	159	210
µg. P per mg. dry wt.	0.63	1.67	2.06

ments with the spectrophotometric test of succinic dehydrogenase activity shown to be more sensitive (Stafford 1951).

Discussion. Very few reports have been made on the distribution of enzymes within plants. Engel (1947) found that proteinase, dipeptidase, and esterase in cereal grains are predominantly in the aleurone cells and only slightly in the endosperm. In wheat seeds, β-amylase is not in the aleurone layer, but is rich in the layer just below (first starch layer) and is present in only a moderate amount of the inner endosperm. Upon germination, it is located in the scutellum (Engel & Bretschneider 1947). Amylase studies are difficult not only because of the possible presence of different types of amylases, but because of the presence of bound and unbound or active and inactive forms which are activated by treatment with papain. The present study was concerned with an α-amylase, but no attempt was made to determine the presence of a bound form.

Certain precautions must be considered in any developmental or distribution study. With all these enzymes, the absence or lessened activity in the seed as compared with the seedling or in a comparison between regions could be due to a lack of the enzyme, or to its being in an inactive form. The increase in activity of an enzyme upon germination, therefore, may be a result of a synthesis of new enzyme or the activation of an already formed supply by removal of an inhibitor or by release from a bound state. The data presented here do not differentiate between these possibilities.

The above study could provide misleading data because the relative amounts of inactive material might vary as is probably the case with the amount of storage protein and starch in the cotyledons, or the sample of the ungerminated seeds might include some non-viable seeds which would be excluded at the older age. The predominance of a particular enzyme, like ascorbic oxidase, in the root-shoot axis could lead one to believe that an enzyme was missing at a young seedling stage, but the effect might be one of dilution rather than one of a lack. A study of the distribution of enzymes within a plant, therefore, is of value in a developmental study. It is also important to express the data in various ways because the distribution may vary when based on wet weight, dry weight or protein values.

References in the literature to developmental studies of enzymes are more numerous than those on the distribution within the plant. Most workers have used legumes or grasses as experimental material. According to Davison (1949) cytochrome oxidase is the terminal enzyme in seeds, but the activity falls off upon germination, and ascorbic oxidase takes its place. This concept is based on inhibitor experiments on a rather small endogenous respiration involving small percentage differences. The present investigation confirms the increase in ascorbic oxidase upon germination, but shows no dropping off of the cytochrome oxidase activity, but in fact, shows an increase. The increase in cytochrome oxidase was much steeper than for succinoxidase, but the latter was less stable. This would not lower the ratio of cytochrome oxidase to succinic dehydrogenase at this seedling stage as shown by Albaum, Novikoff and Ogur (1946) for developing chicken embryos.

According to Rangnekar and Suvrahmanyar (1948), ascorbic oxidase in soybeans reached a maximum at 48 hours after germination, and then remained constant in the cotyledons and decreased in the sprout. Shen, Hsieh and Chen (1945) reported an increase in ascorbic acid content and oxidase during germination in soybeans but at different rates. The activity of the oxidase in the sprout was much greater and increased with age than in the cotyledons, while the reverse was true of ascorbic acid. The present data confirm this increase.

Labarre and Pfeffer (1946) stated that in *Vicia faba* there are two amylases which reach their maximum activity 8 to 10 days after germination. Similar increases with subsequent decreases were reported by Roca and Ondarza (1948) in *Phaseolus vulgaris* and by Bach, Oparin and Wähner (1927). The data for peas confirm this increase also.

SUMMARY

1. Five enzymes from pea homogenates were studied in respect to their distribution between the cotyledons and the root-shoot axis and to their development during germination up to 6 day-old seedlings.

2. When the activity is expressed in terms of wet weight, ascorbic oxidase occurred predominantly in the root-shoot axis, while amylase was equally distributed between the two regions, and cytochrome oxidase, succinoxidase, and phosphorylase were primarily found in the cotyledons. When compared in terms of dry weight or protein, ascorbic oxidase, cytochrome oxidase, and amylase activities were now more concentrated in the root-shoot axis, and phosphorylase and succinoxidase were more concentrated in the cotyledons.

3. All of the above enzymes except ascorbic oxidase were found in ungerminated seeds, and all increased in activity upon germination.

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NEW SOUTH AMERICAN UMBELLIFERAE

MILDRED E. MATHIAS AND LINCOLN CONSTANCE

The detection of the three genera and three species described below as new was essentially a by-product of a revisionary study of the genus *Niphogeton* Schlecht., to be published shortly by the University of California Press.* *Cotopaxia* and *Perissocoeleum* appeared as "contaminants" in the collections generously loaned by the Royal Botanic Gardens, Kew, and other institutions. In attempting to delimit *Perissocoeleum* from all possible relatives, it was necessary to inquire into the affinities of *Peucedanum oreopansil* Griseb., which led to the proposal of *Austropeucedanum* as a distinct genus. Finally, the remarkable *Prionosciadium phylloideum* turned up, quite unexpectedly, in the search for additional material of *Niphogeton* in the collections of the wartime Colombian Cinchona Mission.

There has never been any general treatise on the Umbelliferae in South America, and it therefore seems probable that many types presently unknown will be found to occur there. In order to be sure that we have not duplicated any of the widely scattered descriptions of new taxa, we have attempted to accumulate all of the original descriptions. Although the identity of some of the genera and species previously proposed by others—such as *Azorellopsis* Wolff and *Paraselinum* Wolff—is obscure to us and may remain so indefinitely with the destruction of the Berlin herbarium, we are satisfied that we have avoided duplicating any of them in our new proposals.

Whenever workers concerned with a particular group in a particular continent extend their study to a different land mass, it is only natural that their new study should be based upon their previous ones. Thus, we undoubtedly approach the Umbelliferae of South America with a decided North American bias, just as European workers approached the representatives of the family in North America. The resultant tendency is ordinarily to refer new forms to well-established "form-genera;" later, the pendulum is apt to swing too far in emphasizing local peculiarities, leading to the over-propagation of small and ill-defined genera. Recognizing our own bias, we are attempting to steer a middle course, which may well result in our erring in both directions simultaneously.

The decision to increase the number of genera has not been reached lightly. Treating the whole of the North American representation of the same family, we found it necessary to describe only a single genus. We have,

* A revision of the Andean genus Niphogeton (Umbelliferae); Univ. Calif. Publ. Bot. 23(9): 405–426. 1951.

however, arrived independently at the decision that to combine any of the plants on which the following proposed genera are based with any known American genus, or with each other, would result in unnecessarily obscuring their characteristics. The collection and comparison of extensive additional material will determine, in due course, whether or not our present disposition was a wise one.

Perissocoeleum Mathias and Constance, gen. nov. Herbae perennes crassae erectae caulescentes ramosae glabrae puberulentaeve radice nobis ignota. Folia petiolata subcoriacea pinnato-decomposita divisionibus integris; petioli vaginantes supra auriculati. Inflorescentiae umbellae compositae laxae; pedunculi terminales axillaresque laminis longiores; involucri bractae plures pinnatifidi radiis breviores; radii pauci patenti-adscendentes; involucelli bracteolae plures integrae trifidaeve flores subaequantes; pedicelli graciles patenti-adscendentes. Flores albi nervo medio colorato; petala lanceolata acuta apicibus haud inflexis; calycis dentes obsoleti; stylopodium conicum stylis brevibus patentibus; carpophorum nobis ignotum. Fructus oblongus, dorsaliter valde compressus glaber; costae dorsales filiformes; alae laterales membranaceae corporem subaequantes; vittae magnae in intervallis solitariae, in commissura duae; seminum dorsaliter complanatum, sub intervallis sulcatum facia planum.

Stout, erect, succulent, herbaceous, caulescent, branching, glabrous or sparsely scaberulous or puberulent perennial, the root unknown. Leaves petiolate, subcoriaceous, pinnately decompound, the divisions entire. Petioles sheathing, auriculate above. Inflorescence of loose compound umbels; peduncles terminal and lateral, longer than the leaves. Involucre of several pinnatifid bracts, shorter than the rays. Rays rather few, spreading-ascending. Involucel of several linear, entire or trifid bractlets, about equaling the flowers. Pedicels slender, spreading-ascending. Flowers white with a colored midvein; petals lanceolate, acute, the apex incurved (but not sharply inflexed); calyx teeth obsolete; styles short, spreading, the stylopodium conical. Carpophore unknown. Fruit oblong, strongly flattened dorsally, glabrous; dorsal ribs filiform, the lateral with membranous wings about equaling the body; vittae rather large, solitary in the intervals, 2 on the commissure; seed flattened dorsally in cross section, sulcate beneath the intervals, the face plane.

TYPE SPECIES, **Perissocoeleum Purdiei** Mathias and Constance.

Perissocoeleum Purdiei Mathias and Constance, sp. nov. (fig. 1.) Herba 3–4 dm. alta apud inflorescentian scaberula puberulave supra basim ramis adscendentibus ramosa foliis basilaribus ovatis 6–10 cm. longis 4–7 cm. latis divisionibus ultimis lineari-filiformibus rigidibus mucronatis 1–5 mm. longis 0.5 mm. latis petiolis crassis valde inflatis 10–12 cm. longis basi vaginantis pedunculis 5–15 cm. longis infra umbellas scaberulis puberulisve involucri bracteis 5–8 linearibus spatulatisve pinnatisectis vel raro integris 8–15 mm. longis radiis plerumque brevioribus radiis 8–15 gracilibus adscendentibus inaequalibus 1.5–3.5 cm. longis involucelli bracteolis 8–12 linearibus integris trifidisque 4–8 mm. longis basi paullo connatis pedicellos aequantibus pedicellis 8–12 inaequalibus 4–8 mm. longis staminibus exsertis stylis patentibus ca. 0.2 mm. longis fructu apice basique rotundato glabro 5–6 mm. longo 2–2.5 mm. lato.

FIG. 1. **Perissocoeleum Purdiei.** a. Habit, × 2/3. b. Lower cauline leaf, × 2/3. c. Umbellet, × 1 1/3. d. Petals, × 8. e. Fruit, side view, × 6. f. Fruit, transverse section, × 8.

Plants 3–4 dm. tall, branching above the base, the branches ascending, the foliage glabrous, the inflorescence scaberulous or puberulent; basal leaves ovate, 6–10 cm. long, 3–4 cm. broad, the ultimate divisions linear-filiform, rigid, 1–5 mm. long, up to 0.5 mm. broad, mucronate, the petioles stout, 10–12 cm. long, the lower two-thirds to four-fifths forming an obovate, scarious-winged sheath, the upper petioles obovate, dilated, wholly sheathing, and the blades greatly reduced; inflorescence terminal and lateral, the peduncles 5–15 cm. long, scaberulous or puberulent beneath the umbel; involucre of 5–8 linear to spatulate, pinnatifid or rarely entire bracts 8–15 mm. long, usually shorter than the rays; rays 8–15, 1.5–3.5 cm. long, slender, ascending, unequal; involucel of 8–12 linear bractlets like the bracts, entire or trifid, 4–8 mm. long, slightly connate at the base, about equaling the pedicels; pedicels 8–12, 4–8 mm. long, unequal; petals white with a colored midvein; stamens exserted; styles ca. 0.2 mm. long, spreading; fruit 5–6 mm. long, 2–2.5 mm. broad, rounded at the apex and base, glabrous.

TYPE LOCALITY: "High mountains of the Nevada de Santa Marta," Colombia, July, 1844, *William Purdie* (K: type). (For a biographical account of the collector, see Ewan (1948).)

DISTRIBUTION: Known only from the Sierra Nevada de Santa Marta, Colombia.

SPECIMENS EXAMINED: COLOMBIA. Magdalena: Nevada de Santa Marta, 1844, *Purdie* (K: type), 1845, *Purdie* (K); páramos of the Sierra Nevada de Santa Marta about 30 miles inland from Dibulla, alt. ca. 4390 m., July, 1932, *Seifriz 497* (US).

With its dorsally flattened, peucedanoid fruit, *Perissocoeleum* is comparable in South America only with the genera *Prionosciadium, Myrrhidendron,* and *Austropeucedanum* and in North America possibly with *Rhodosciadium*. The prominently involucrate umbels and the lack of an inflexed petal apex, as well as habit, distinguish it sharply from *Myrrhidendron, Austropeucedanum,* and *Rhodosciadium,* and the conical stylopodium from *Prionosciadium*. The carpophore cannot be clearly made out in the available fruiting material (more than a century old), but this structure appears to break through at the base so that the mericarps do not separate at maturity in the usual fashion. Better fruiting specimens are needed to settle this point.

The new genus is known only from the isolated Sierra Nevada de Santa Marta, which have proven to have a remarkable flora of Umbelliferae. From this range have already been described *Hydrocotyle grossulariaefolia* Rusby, *H. heucheraefolia* Mathias, *Micropleura flabellifolia* Mathias, and *Prionosciadium crinoideum* Math. & Const. The name of the genus is derived from the words περισσός, exaggerate, and κοῖλος, sheath, in recognition of the distinctively dilated sheaths of the cauline leaves.

Cotopaxia Mathias and Constance, gen. nov. Herbae perennes graciles erectae caulescentes ramosae scaberulosae e radicibus napiformibus. Folia petiolata membranacea pinnato-decomposita divisionibus ultimis integris; petioli vaginanti. Inflorescentae umbellae compositae laxae; pedunculi ter-

minales axillaresque laminis longiores; involucri bractae paucae lineariae ovataeve integrae vaginantae; radii pauci patenti-adscendentes; involucellus dimidiatus bracteolis paucis linearibus integris basi connatis floribus brevioribus; pedicelli breves patenti-adscendentes. Flores albi; petala ovalia acuta apicibus haud inflexa; calycis dentes obsoleti; stylopodium nullum stylis gracilibus patentibus; carpophorum bipartitum ramis filiformibus. Fructus oblongo-ovoideus, lateraliter paullo compressus subteretusve glaber; costae omniae anguste alatae; vittae in intervallis solitariae, in commissura duae; seminum paullo dorsaliter complanatum, sub intervallis sulcatum facie plana concavumve.

Slender, erect, herbaceous, caulescent, branching, scaberulous perennial, from a napiform root. Leaves petiolate, membranaceous, pinnately decompound, the ultimate divisions entire. Petioles sheathing. Inflorescence of loose compound umbels; peduncles terminal and lateral, longer than the leaves. Involucre of one to several linear to ovate, entire, inconspicuous, sheathing bracts. Rays rather few, spreading-ascending. Involucel dimidiate, of a few linear, entire bractlets connate at the base, shorter than the flowers. Pedicels short, spreading-ascending. Flowers white; petals oval, acute, the apex not inflexed; calyx teeth obsolete; styles slender, spreading, the stylopodium lacking. Carpophore divided to the base, its branches filiform. Fruit oblong-ovoid, slightly flattened laterally or subterete, glabrous; all the ribs narrowly winged; vittae solitary in the intervals, 2 on the commissure; seed somewhat dorsally flattened in cross section, sulcate beneath the intervals, the face plane or shallowly concave.

TYPE SPECIES, **Cotopaxia Asplundii** Mathias and Constance.

Cotopaxia Asplundii Mathias and Constance, sp. nov. (fig. 2.) Herba scaberula basi vel supra basim ramosa 1.7–6.3 dm. alta foliis basilaribus paullo confertis ovato-lanceolatis 2–7 cm. longis 1–4 cm. latis divisionibus ultimis linearibus lanceolatisve acuminatis 1–4 mm. longis usque ad 1 mm. latis petiolis gracilibus 3–10 cm. longis basi vaginantis pedunculis plerumque 2–6 cm. longis infra umbellas scabris involucri bracteis scarioso-vaginantis 2–7 mm. longis radiis plerumque brevioribus radiis 10–15 patenti-adscendentibus inaequalibus scaberulis 5–30 cm. longis involucelli bracteolis 3–6 linearibus scarioso-marginatis scaberulis 2–6 mm. longis basi paullo connatis floribus brevioribus pedicellis 6–15 inaequalibus 2–6 mm. longis petalis albis nervo medio flavido staminibus exsertis stylis 1–3 mm. longis fructu ca. 4 mm. longo 1.5–2 mm. lato costis omnibus anguste alatis acutis lateralibus dorsalibus paullo longioribus vittis magnis lunatis.

Plants 1.7–6.3 dm. tall, branching at or above the base, the branches ascending; foliage light green, the leaves loosely clustered toward the base, ovate-lanceolate, 2–7 cm. long, 1–4 cm. broad, the ultimate divisions linear or lanceolate, acuminate, 1–4 mm. long, up to 1 mm. broad, the petioles slender, 3–10 cm. long, the lower one-fifth to one-third in the basal leaves forming a broadly oblong, scarious-winged sheath, the upper petioles obovate, dilated, wholly sheathing; inflorescence terminal and lateral, with one to several lateral peduncles arising in the axils of the upper cauline leaves, 2–20 cm. long, densely scabrous beneath the umbel; involucre of one to several scarious-sheathing bracts 2–10 mm. long, usually shorter than the rays; rays 10–15, 5–30 cm. long, unequal, scaberulous; involucel of 3–6 linear, scarious-margined, scaberulous bractlets 2–6 mm. long, slightly con-

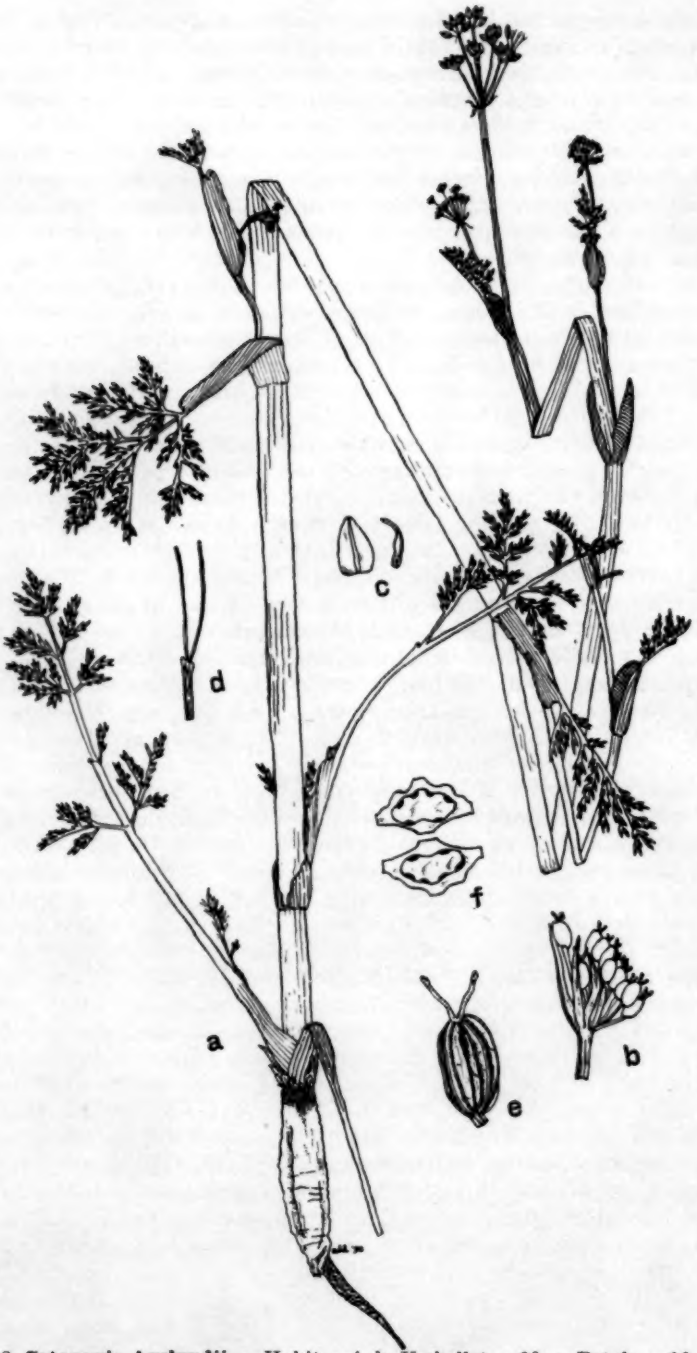

FIG. 2. **Cotopaxia Asplundii**. a. Habit, × ⅔. b. Umbellet, × 2⅔. c. Petals, × 10. d. Carpophore, × 5. e. Fruit, side view, × 5. f. Fruit, transverse section, × 10.

nate at the base, shorter than the flowers; pedicels 6–15, 2–6 mm. long, unequal; petals white with a yellowish midvein; stamens exserted; styles 1–1.3 mm. long; fruit ca. 4 mm. long, 1.5–2 mm. broad, all the ribs narrowly winged, acute, the lateral a little longer than the dorsal; vittae large, lunate.

TYPE LOCALITY: "Railway station Cotopaxi, páramo, alt. 3500 m.," 26 May 1939, *Erik Asplund 6469* (S: type).

DISTRIBUTION: Known only from páramos at 10,–13,000 feet altitude of Cerro Cotopaxi, Ecuador, for which the genus is named.

SPECIMENS EXAMINED: ECUADOR. Cotopaxi: Cotopaxi, *W. Jameson 121* (K,LA); Railway station Cotopaxi, páramo, *E. Asplund 6469* (S: type; US; NY,UC-photos); "Quito," *W. Jameson 32* (G, w).

Superficially similar to *Niphogeton scabra* (Wolff) F. Macbr., *N. stricta* (Wolff) Math. & Const., and *N. dissecta* (Benth.) F. Macbr., with the last of which it was apparently confused by Bentham, *Cotopaxia* differs markedly by its dorsally compressed mericarps, its lack of a stylopodium, and by its carpophore branches. The statement by Bentham (1867) under *Oreosciadium* (= *Niphogeton*) that, "*O. dissectum*, Wedd., anomalum est, fructu fere *Seselios* a latere vix compresso, jugis lateralibus crassioribus, et semine a dorso compresso, facie concaviusculo" probably relates at least in part to *Cotopaxia*. The Kew specimens of *Cotopaxia* are mounted on the same sheet as the type collection of *Petroselinum dissectum* Benth. (the basis of *Oreosciadium dissectum* Wedd.), and Bentham apparently had no fruiting material of the latter.

We have been unable to discover any genus hitherto reported from the South American continent to which the present material might be referred. A comparison with the various sections of our generic key to the North American Umbelliferae (1944–45) appears to lead to the genera *Musineon* Raf., *Aletes* Coult. & Rose, *Ligusticum* L., and *Pseudocymopterus* Coult. & Rose. From *Musineon* and *Aletes* the new genus differs in habit, petal apex, lack of evident calyx teeth, and the nature of the carpophore. The lack of either an inflexed petal apex or a stylopodium distinguishes it from *Ligusticum;* the possession of an involucre, the color of the petals and their lack of an inflexed apex, the want of evident calyx teeth, and the uniform prominence of the dorsal fruit ribs sets it apart from *Pseudocymopterus.*

It is a pleasure to designate the species for Dr. Erik Asplund, whose extensive botanical work in the South American cordillera has provided such excellent herbarium material. We are especially grateful to him for the opportunity of examining his interesting set of Umbelliferae.

Austrocaucedanum Mathias and Constance, gen. nov. Herbae biennes (?) elatae caulescentes ramosae scabrae e radicibus napiformibus. Folia petiolata membranacea pinnato-decomposita divisionibus integris vel serratis lobatisve confluentibus; petioli vaginanti. Inflorescentiae umbellae compositae laxae; pedunculi terminales axillaresque laminis longiores; involucri bractae paucae nullaeve integri radiis breviores; radii plures patenti-adscendentes; involucelli bracteolae plures lineares integrae floribus ple-

rumque breviores; pedicelli graciles patenti-adscendentes. Flores albi; petala obovata emarginata apicibus angustioribus inflexa; calycis dentes obsoleti; stylopodium breviter conicum stylis brevibus patentibus; carpophorum bipartitum ramis filiformibus. Fructus oblongus, dorsaliter valde compressus glaber; costae dorsales filiformes; alae laterales membranaceae corporem subaequantes; vittae magnae in intervallis solitariae in commissura duae; seminum dorsaliter complanatum sub intervallis sulcatum facie planum.

Tall, herbaceous, caulescent, branching, scabrous biennial (?), from a napiform taproot. Leaves petiolate, membranaceous, pinnately decompound, the divisions entire, serrate or lobed, confluent. Petioles sheathing. Inflorescence of loose compound umbels; peduncles terminal and lateral, longer than the leaves. Involucre of 1 or 2 filiform bracts or wanting. Flowers white; petals obovate, emarginate, with an inflexed apex; calyx teeth obsolete; styles short, spreading, the stylopodium low-conic. Carpophore divided to the base, its branches filiform. Fruit oblong, strongly flattened dorsally, glabrous; dorsal ribs filiform, the lateral with membranous wings about equaling the body; vittae rather large, solitary in the intervals, 2 on the commissure; seed flattened dorsally in cross section, sulcate beneath the intervals, the face plane.

TYPE SPECIES, *Peucedanum oreopansil* Griseb. (*Austropeucedanum oreopansil* Mathias and Constance).

Austropeucedanum orecpansil (Griseb.) Mathias and Constance, comb. nov. (fig. 3.) *Peucedanum oreopansil* Griseb. Symb. Fl. Argent. 147. 1879.

TYPE LOCALITY: "Cuesta del Garabatal, in regione Aliso cum Escalloniis in locis humidis," Tucuman, Argentina, *Lorentz & Hieronymus 884.*

DISTRIBUTION: Mountains of northwestern Argentina.

SPECIMENS EXAMINED: ARGENTINA. Río Negro: Region of Lago Nahuel Huapi, *I. R. Cordini 225* (US). Tucuman: Gebirgs zug der Cuesta del Garabatal, Sierra de Tucuman, January, 1874, *Lorentz & Hieronymus 880* (F); Sierra de Tucuman, *Lorentz & Hieronymus 667* (F, US); San Javier: San Pablo, 1200 m., 15 December 1905, *M. Lillo 4564* (UC); Chicligasta, Las Pavas, 3200 m., 12 May 1924, *S. Venturi 3072* (GH, US).

The occurrence of a single species of "*Peucedanum*" in southern South America, with all the rest of this large genus in the Old World, has long seemed anomalous. The North American plants once referred to "*Peucedanum*" were long ago distributed among *Prionosciadium, Rhodosciadium, Oxypolis,* and *Lomatium.* According to Thellung's key to the natural groups of the genus *Peucedanum* (1926), *Austropeucedanum* would come nearest Subgen. I. *Imperatoria,* which has frequently been recognized as a distinct Linnean genus. There is a decided lack of precise technical characters to separate the two, but the difference in duration, habit, foliage, fruit shape, and the greater development of stylopodium in the European plant, together with the great geographical separation of the two, appear to make generic segregation warranted. Of American genera, *Austropeucedanum* appears to be most closely related to *Rhodosciadium* and *Prionosciadium.* From the former it differs in flower color, shape of fruit, and the charac-

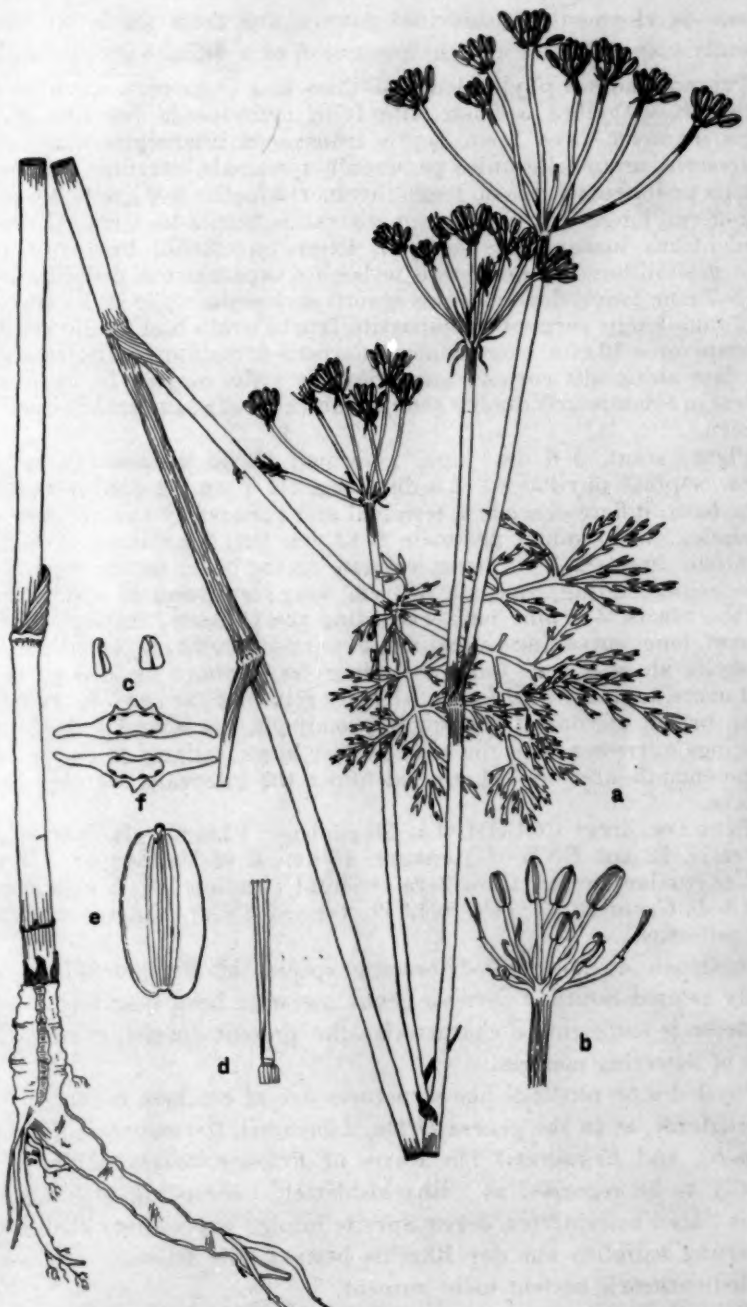

FIG. 3. **Austropeucedanum oreopansil.** a. Habit, × ⅓. b. Umbellet, × 1¾. c. Petals, × 6. d. Carpophore, × 5½. e. Fruit, side view, × 5. f. Fruit, transverse section, × 10.

teristic development of unisexual flowers, and from the latter in the apparently biennial habit and the possession of a definite stylopodium.

Prionosciadium phylloideum Mathias and Constance, sp. nov. (fig. 4.) Herba crassa glabra 5–6 dm. alta foliis cylindraceis fistulosis 2–2.5 dm. longis diametro circa 1 cm. septis transversis interceptis basi vaginantis inflorescentiae umbello unico pedunculis terminals interdum lateralibus instructis pedunculo 8–12 cm. longo involucri bracteis 6–8 linearibus acuminatis 2–3 cm. longis basi valde connatis radiis fertilibus circa 20 patenti-adscendentibus inaequalibus 3–4 cm. longis involucelli bracteolis pluribus bracteis similibus 3–5 mm. longis pedicellos superantibus pedcellis fertilibus 3–5 5–7 mm. longis floribus nobis ignotis stylopodio nullo stylis adscendentibus 2 mm. longis carpophoro bipartito fructu ovato basi paullo retuso apice truncato circa 10 mm. longo 5 mm. lato costis dorsalibus valde crassis lateralibus late alatis alis corpore angustioribus vittis magnis in valleculis solitaribus in commissuris duobus semino sub valleculis canaliculato facie parum concavo.

Plants stout, 5–6 dm. high, glabrous; leaves reduced to cylindrical, hollow, septate phyllodes 2–2.5 dm. long, ca. 1 cm. in diameter, sheathing at the base; inflorescence of a terminal and apparently one or more axillary peduncles, the terminal peduncle 8–12 cm. long; involucre of 6–8 linear, acuminate bracts 2–3 cm. long, connate at the base; fertile rays about 20, spreading-ascending, unequal, 3–4 cm. long; involucel of several bractlets like the bracts, 3–5 mm. long, exceeding the pedicels; fertile pedicels 3–5, 5–7 mm. long, spreading-ascending; flowers unknown; stylopodium lacking, the styles about 2 mm. long, ascending; carpophore divided to the base; fruit ovate, truncate at the apex, slightly retuse at the base, ca. 10 mm. long, 5 mm. broad, the dorsal ribs thick, prominent, the lateral broadly winged, the wings narrower than the body; vittae large, solitary in the intervals, 2 on the commissure; seed channeled under the intervals, the face shallowly concave.

TYPE LOCALITY: COLOMBIA. Magdalena: Páramo, alt. 3000 m., Sierra de Perija, 12 km. ENE of Manaure, 48 km. E of Valldeupar, 1 km. from the Venezuelan border, Cordillera Oriental [Station 12], 5 February 1945, *Martin L. Grant 10,857* (UC 901,849: type; USNA). Known only from the type collection.

Inasmuch as no phyllode-bearing species of *Prionosciadium* or any closely related South American genus has ever been described, the foliar character is sufficient to characterize the present species, even in the absence of flowering material.

Phyllodes or phyllode-like structures are of common occurrence in the Umbelliferae, as in the genera *Ottoa, Lilaeopsis, Oreomyrrhis, Ptilimnium, Oxypolis,* and *Eryngium.* The leaves of *Prionosciadium phylloideum* are actually to be regarded as "Rhachisblätter," according to Troll (1934), that is "als Fiederblätter, deren Spreite infolge von völliger Reduktion der Fiederung lediglich aus der Rhachis bestaht. Die teilweise angenommene Phyllodientheorie besteht nicht zurecht."

We wish to express our thanks to Dr. Rimo Bacigalupi, Curator of the

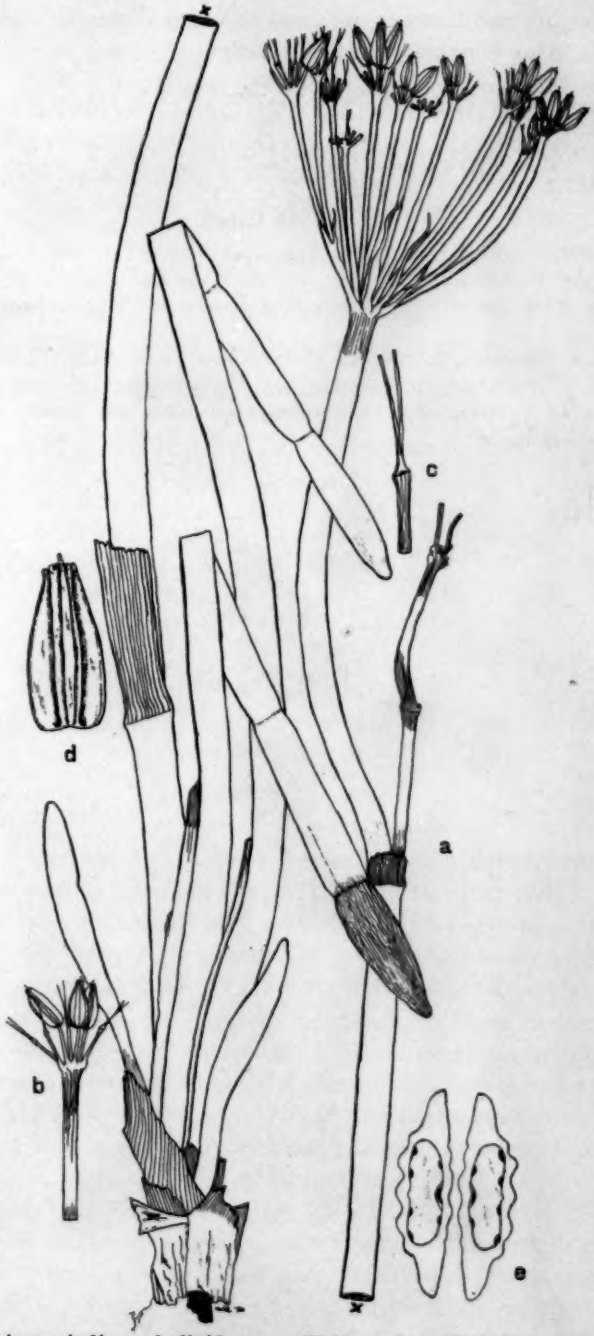

FIG. 4. **Prionosciadium phylloideum**. a. Habit, × ⅜. b. Umbellet, × 1½. c. Carpophore, × 2. d. Fruit, side view, × 2½. e. Fruit, transverse section × 7½.

Jepson Herbarium and Library, who assisted very materially with the Latin diagnoses. Mr. Alex Hawkes prepared the figures.

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A COMPARISON OF THE THREE-DIMENSIONAL SHAPES OF CORK CAMBIUM AND CORK CELLS IN THE STEM OF PRELARGONIUM HORTORUM BAILEY (CONCLUDED)

FRANK G. LIER

The 8 most frequently recurring combinations in the cork and cork cambium cells are entered in table 5. There were 2 combinations which occurred

TABLE 5. *The 8 most frequently occurring combinations in 100 cork and 100 cork cambium cells.*

No. of sides per face				Total faces	No. of cells		No. of arrangements found	No. of mirror image pairs
4	5	6	7		Cork	Cork cambium		
4	4	6	.....	14	9	.....	3	.....
3	6	2	.....	11	7	2	1	4
4	4	4	.....	12	8	.....	3	3
4	4	5	.....	13	6	2	3	.....
3	6	4	.....	13	4	2	3	1
3	6	6	.....	15	4	.....	3	.....
5	4	4	2	15	.....	3	2	1
2	8	3	.....	13	.....	3	2	.....
					—	—	—	—
Totals					38	12	20	9

9 times. One of these had 4 quadrilaterals, 4 pentagons, and 6 hexagons (4–4–6). This combination occurred 9 times in the cork cells, 5 times in the cells derived from an anticlinally undivided cork cambium cell (figs. 28 & 29), and 4 times from a cork cambium cell which had undergone an anticlinal division (figs. 30 & 31). This particular combination did not occur in the cork cambium cells. The arrangements of the faces on these cells were studied from conventional models by a technique described in a previous paper by Matzke (1948). The faces of the 9 cells existed in 3 arrangements. There were 2 series of 4 identical cells giving 2 arrangements, and a single cell in a third arrangement. In the cork tissue there were eleven 14-faceted cells; 9 of them had the 4–4–6 combination of faces. In cork cambium 2 cells had a 4–6–2–2 combination (figs. 21 & 22). This was the only repeated combination in thirteen 14-faceted cells found in the cork cambium tissue.

The other combination, which also occurred 9 times, consisted of 3 quadrilaterals, 6 pentagons, and 2 hexagons (3–6–2). Seven cork cells had this combination, and all these cells were derived from a cork cambium cell

which had undergone an anticlinal division (figs. 32, 33 & 35–37); two dividing cork cambium cells also had this combination of faces (figs. 19 & 20). This combination existed in only one arrangement of faces. In the cork cambium 7 cells had 11 faces, and of these, 2 had the 3–6–2 combination: in the cork cells the 3–6–2 combination occurred in 7 of the 11 cells with 11 faces.

An analysis of the kinds of faces found in the tangential, radial, and top and bottom faces in cells possessing the 4–4–6 and the 3–6–2 combination resulted in the data shown in table 6. In the tangential surfaces of the cells

TABLE 6. *Kinds of faces in tangential, radial, top and bottom surfaces of the two most frequently occurring combinations of faces in cork and cork cambium cells. Each figure represents 1 face: 4 (quadrilateral), 5 (pentagon), 6 (hexagon).*

Kind of cell	Tangential surfaces		Radial surfaces		Top surface	Bottom surface
			4–4–6 Combination			
Cork	6	6	5564	5546	46	64
"	6	6	6446	4655	46	55
"	6	6	5546	6446	46	55
"	6	6	4655	6455	46	64
"	6	6	6446	5555	46	64
"	6	6	46	46	5555	4664
"	6	6	6455	4655	46	46
"	5	5	46466	56	65	464
"	6	6	4664	5555	46	64
			3–6–2 Combination			
Cork cambium	5	5	4555	45	6	46
" "	5	5	6	6455	45	45
Cork	5	5	6	55	45	6445
"	5	5	4564	45	6	55
"	5	5	55	45	46	456
"	5	5	46	456	45	55
"	5	5	4655	6	45	45
"	5	5	45	45	6	4655
"	5	5	456	46	45	55

bearing the 4–4–6 combination, it is readily seen that the usual type of face was a hexagon. In the 3–6–2 combination the tangential surface was a pentagon. Although there were actually only 4 out of 18 surfaces which had the 4, 6, 6, 4 pattern in the 4–4–6 combination, i.e., 2 quadrilaterals and 2 hexagons alternating with each other, the other 4-faceted surfaces had patterns which hovered around it. Most of the radial surfaces had 4 faces (14 out of 18 surfaces). The top and bottom surfaces consisted mainly of 2 faces (15 out of 18 surfaces); these were chiefly made up of a quadrilateral and a hexagon (12 out of 18 surfaces). In the 3–6–2 combination the radial faces showed greater variability in the number of faces per surface, having

1, 2, or 4 faces per surface. The same was true for the top and bottom surfaces of these cells.

A combination of 4 quadrilaterals, 4 pentagons, and 4 hexagons occurred 8 times. All of the cells exhibiting this combination were cork cells, 5 of them being derived from undivided cork cambium cells and 3 from anticlinally divided cork cambium cells. The faces of the cells showing this combination were arranged in 3 ways.

Two combinations of faces, those with 5 quadrilateral, 4 pentagonal, 4 hexagonal, and 2 heptagonal faces (5–4–4–2) (figs. 26 & 27) and those with 2 quadrilateral, 8 pentagonal, and 3 hexagonal faces (2–8–3) (figs. 23 & 24) each occurred 3 times and were the combinations which were most frequent in the cork cambium cells. One non-dividing and two dividing cells were found containing each of these combinations. Cells possessing the 5–4–4–2 combination of faces had these faces in 2 arrangements, one consisting of a pair of cells whose faces were in mirror image arrangement. Cells with the 2–8–3 combination also existed in 2 arrangements, 2 of the cells being identical and the other differing in arrangement of faces from these two.

The 8 most frequently occurring combinations of faces exhibited 20 arrangements of those faces.

When cork cambium or cork cells were studied in transverse section three positions of faces were discernible, namely faces on the 2 tangential surfaces, 2 radial surfaces, a top, and a bottom surface. An analysis of the

TABLE 7. *Kinds of faces on 50 dividing and 50 non-dividing cork cambium cells.*

Sides per face	Tangential faces				Radial faces				Top and bottom			
	Dividing cells		Non-div. cells		Dividing cells		Non-div. cells		Dividing cells		Non-div. cells	
	No.	% of tot.	No.	% of tot.	No.	% of tot.	No.	% of tot.	No.	% of tot.	No.	% of tot.
2	.....	.....	.....	.....	1	0.2	4	1.1	.....	.....	.....	.....
3	1	0.9	.....	.....	23	5.5	27	7.2	3	1.4	18	9.2
4	6	5.7	1	1.0	115	27.5	121	32.2	66	29.7	60	30.8
5	31	29.3	15	14.7	153	36.6	115	30.6	69	31.2	72	36.9
6	40	37.7	39	38.2	93	22.3	87	23.1	56	25.2	36	18.5
7	20	18.9	27	26.5	28	6.7	18	4.8	24	10.8	6	3.1
8	6	5.7	15	14.7	4	1.0	2	0.5	4	1.8	3	1.5
9	1	0.9	4	3.9	1	0.2	2	0.5	.....	.....	.....	.....
10	1	0.9	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
11	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
12	.....	.....	1	1.0	.....	.....	.....	.....	.....	.....	.....	.....
Total	106		102		418		376		222		195	
Total for each surface		208				794				417		

kinds of faces on each of the surfaces of the dividing and non-dividing cork cambium cells and their frequency of occurrence yields the data summarized in table 7. An inspection of this table reveals that on the tangential surfaces, hexagonal faces predominated on both the dividing and the non-dividing cells, accounting for 38 per cent of all the tangential faces in both cases. On the radial surfaces, pentagons predominated in the dividing cells, being 37 per cent of all the radial faces. In the non-dividing cells, however, quadrilateral faces predominated accounting for 32 per cent of the total number of radial faces. The most frequently occurring face on both the top and bottom surfaces of the dividing and non-dividing cork cambium cells was the pentagon, accounting for 31 and 37 per cent respectively of all the top and bottom faces.

The average number of faces for each of the surfaces of the cork cambium cells is summarized in table 8. The data for all the cork cambium cells

TABLE 8. *Average number of faces per surface in 100 cork cambium cells.*

	All cells		Dividing cells		Non-dividing cells	
	Total faces	Average per cell	Total faces	Average per cell	Total faces	Average per cell
Tangential surface	208	2.08 [0.31]*	106	2.12 [0.38]*	102	2.04 [0.20]*
Radial surface	794	7.94 [1.77]	418	8.36 [2.02]	376	7.52 [1.45]
Top and bottom surface	417	4.17 [1.37]	222	4.44 [1.48]	195	3.90 [1.22]
Average faces per cell (rounded off)		14		14		14

* Standard deviation of data.

indicated that, on the average, each tangential surface consisted of one face (2.08 or 2 faces for 2 tangential surfaces), each radial surface of 4 faces (7.94 or 8 faces for 2 radial surfaces), the top surface and the bottom surface of 2 faces each (4.17 or 4 faces for both the top and bottom surface). Strictly on an average basis then, the total number of faces on a cork cambium cell is 14.

The increase in the number of faces per radial surface in the dividing cork cambium cells as compared with the non-dividing cells was further illustrated by the fact that 43 of the radial surfaces on the dividing cells had 5 or more faces, while only 20 of the radial surfaces on the non-dividing cells had 5 or more faces. A similar distribution of more faces per surface was shown by the top and bottom surfaces: 32 of such surfaces on the dividing cells had 3 or more faces, while only 20 of the surfaces on the non-

dividing cells had 3 or more faces on those surfaces.

The data for the kinds of faces on tangential, radial, and top and bottom surfaces of cork cells are displayed in table 9. The data for the tangential

TABLE 9. *Kinds of faces on 50 cork cells formed by an anticlinally divided cork cambium cell, and 50 cork cells formed by an undivided cork cambium cell.*

Sides per face	Tangential faces				Radial faces				Top and bottom			
	Cork from divided cork cambium		Cork from un-div. cork cambium		Cork from divided cork cambium		Cork from un-div. cork cambium		Cork from divided cork cambium		Cork from un-div. cork cambium	
	No.	% of tot.	No.	% of tot.	No.	% of tot.	No.	% of tot.	No.	% of tot.	No.	% of tot.
3	.....	.....	.....	.....	9	3.7	4	1.2	2	0.6	.....	.....
4	8	8.0	.....	.....	65	26.6	110	32.6	111	35.8	103	34.7
5	42	42.0	21	20.8	88	35.9	109	32.2	100	32.3	106	35.7
6	34	34.0	46	45.6	77	31.4	107	31.6	92	29.7	81	27.3
7	16	16.0	17	16.8	4	1.6	8	2.4	5	1.6	7	2.3
8	.....	.....	16	15.9	2	0.8	.....	.....	.....	.....	.....	.....
9	.....	.....	1	0.9	.....	.....	.....	.....	.....	.....	.....	.....
Total	100		101		245		338		310		297	
Total for each surface	201				583				607			

surfaces show that pentagonal faces predominate on the surfaces of cells which arise from anticlinally divided cork cambium cells (42 per cent of the total) (figs. 31–33 & 35–37), and that hexagons predominate on the surfaces of the cork cells (46 per cent of the total) which arise from cork cambium cells that had not undergone a previous anticlinal division (figs. 28, 29 & 38). On the radial surfaces of the cork cells, pentagonal faces predominate (36 per cent of the total) on those cells arising from anticlinally divided cork cambium cells, and quadrilaterals are the modal class (33 per cent of the total) in the cork cells from undivided cork cambium cells. Quadrilaterals, pentagons, and hexagons, however, are almost of equal frequency in this latter class. On the top and bottom surfaces quadrilaterals predominate in the cork cells from anticlinally divided cork cambium cells (36 per cent of the total) while pentagons (36 per cent of the total) are most frequent on cells from undivided cork cambium.

The summary of data for the average number of faces per tangential, radial, and top and bottom surfaces of cork cells is presented in table 10. When all the cork cells are considered together, the average number of faces per cell is 14 with the tangential surfaces averaging 2 faces, the radial sur-

TABLE 10. *Average number of faces per surface in 100 cork cells.*

	All cells		Cells from anticlinally divided cork cambium		Cells from anticlinally un-divided cork cambium	
	Total faces	Average per cell	Total faces	Average per cell	Total faces	Average per cell
Tangential surface	201	2.01 [0.10]*	100	2.00 [0.00]*	101	2.02 [0.14]*
Radial surface	583	5.83 [1.76]	245	4.90 [1.20]	338	6.76 [1.76]
Top and bottom surface	607	6.07 [2.16]	310	6.20 [2.21]	297	5.94 [2.11]
Average faces per cell (rounded off)		14		13		15

* Standard deviation of data.

faces 6 faces, and the top and bottom surfaces averaging 6 faces per cell. Even though the average per cell is the same as in the cork cambium cells, the distribution of the faces among the surfaces is different. When the cork cells are divided into the two categories, depending upon whether they arose from an anticlinally divided or undivided cork cambium cell, a difference is evident in the average number of faces per cell. In the cork cells which came from an undivided cork cambium cell, the average number of faces per cell was 15, while the average number of faces on the cork cells which came from a cork cambium cell which had undergone an anticlinal division was 13.

Table 11 shows the actual distribution of the number of faces on cork

TABLE 11. *Number of faces on the tangential, radial, and top and bottom surfaces of cork cambium and cork cells.*

Number of faces per surface	Tangential surface		Radial surface		Top and bottom surface	
	Cork cambium cells	Cork cells	Cork cambium cells	Cork cells	Cork* cambium cells	Cork cells
1	193	199	3	15	33	13
2	6	1	28	81	106	79
3	1	.....	33	31	43	26
4	.....	.....	73	55	7	61
5	.....	.....	39	15	3	14
6	.....	.....	21	3	.....	5
7	.....	.....	1	.....	.....	2
8	.....	.....	2	.....	.....	.....

* Four top and bottom surfaces are replaced by an edge.

cambium and cork cells. In the cork cambium cells the modal class for the tangential surfaces is 1 face per surface, for the radial surfaces 4 faces per surface, and for the top and bottom surfaces 2 faces per surface. The distribution in the cork cells shows that the tangential surface still is predominantly composed of 1 face. In the radial surfaces, however, 2 faces per surface occur more frequently than 4, which here comes second in frequency. The top and bottom surfaces of the cork cells contain 2 faces more often than any other number, with 4 faces being the second most frequent.

The number of faces which any cell possesses is determined, in part, by the divisions of the cells which surround it. The effect of such divisions on the number of faces which any particular cell possesses may readily be studied in the cork tissue. When the cork cells which had come from a cork cambium cell which had not undergone anticlinal division were being studied, it became apparent that there were three classes of these cells which appeared regularly. These depended upon the division pattern of the cork cambium cell above or below the cell being studied. The number of top and bottom surfaces of the cork cells varied in this group, depending upon whether the cork cambium cell above or below had undergone an anticlinal division. The effect of these divisions was to distinguish 3 groups of cells; one group had cork cambium cells above and below which had not divided, the second group had a cork cambium cell above or below which had divided, and the third group had cork cambium cells above and below which had divided. This same pattern was still apparent in the group of cork cells which originated from a cork cambium cell that had undergone an anticlinal division. The radial surfaces of the cork cambium cells above and below

TABLE 12. *Average number of faces on all surfaces of the 3 categories of cork cells described in the text.*

Surface	Radial surface of cell above and below does not intersect tangent. surface		Radial surface of cell above and below intersects tangent. surface		Radial surface of cell above and below intersects tangent. surface	
	Divided cork cambium	Non-div. cork cambium	Divided cork cambium	Non-div. cork cambium	Divided cork cambium	Non-div. cork cambium
Tangential	2.00 [0.00]*	2.05 [0.22]*	2.00 [0.00]*	2.00 [0.00]*	2.00 [0.00]*	2.00 [0.00]*
Radial	5.25 [1.02]	7.50 [1.36]	4.80 [1.48]	6.25 [1.98]	4.60 [1.19]	6.28 [1.73]
Top and bottom	3.85 [0.59]	4.20 [0.77]	6.70 [1.16]	5.87 [1.50]	8.30 [1.03]	8.50 [1.28]
Av-number of faces per cell	11.10 [1.21]	13.75 [1.89]	13.50 [2.32]	14.12 [3.22]	14.90 [1.71]	16.78 [1.72]
Number of cells	20	20	10	16	20	14

* Standard deviation of data.

either did or did not intersect the tangential surfaces on the cells being studied. The same three categories of cells were realized in this group of cork cells as in the former.

Table 12 shows the average number of faces per tangential, radial, and top and bottom surfaces of each of the 3 categories of cells described above. Each of these three categories is further subdivided into cork cells which came from undivided cork cambium cells or cells which had undergone an anticlinal division. The average number of faces per cell can be seen to increase as new contacts are brought to the cells by the anticlinal divisions of the cork cambium cells above and below the cells being studied. In round numbers, the average number of faces on the cork cells which arose from cork cambium cells that had undergone an anticlinal division increases from 11 to 14 to 15 faces per cell as the radial surfaces of cork cambium cells above or below did not intersect, intersected either the top or bottom surface, or intersected both the top and the bottom surfaces of the cells in question. Similarly, the average number of faces on the cork cells which arose from a cork cambium cell which had not undergone an anticlinal division ranged from 14 to 14 to 17 as the radial surfaces of the cells above and below did or did not intersect the cells enumerated in the table.

An analysis of the faces on each of the three kinds of surfaces on both cork and cork cambium cells showed that certain patterns were repeated more frequently than others. A tabulation of those recurring patterns was made for each of the surfaces, and the data are shown in tables 13 and 14.

TABLE 13. *The 16 most frequently recurring patterns of faces on radial surfaces of 100 cork cambium and 100 cork cells.*

Pattern	Cork cambium cells		Cork cells		
	Dividing cells	Non-dividing cells	Anticlinal division in cork cambium	No anticlinal division in cork cambium	Total surfaces
46	4	1	17	11	33
5546	6	4	7	14	31
55	2	4	14	3	23
45	3	4	10	6	23
4664	.....	6	2	11	19
56	2	2	12	3	19
654	1	6	4	6	17
6	2	.....	10	3	15
6445	2	6	2	2	12
5555	2	2	2	3	9
4674	2	4	.....	.....	6
564	1	1	4	.....	6
4554	.....	5	.....	.....	5
644	.....	3	2	.....	5
46456	2	.....	1	1	4
46466	.....	.....	1	3	4

Two other patterns each occurred 3 times.
Nine other patterns each occurred 2 times.

TABLE 14. *The 18 most frequently recurring patterns of faces on the top and bottom surfaces of 100 cork cambium and 100 cork cells.*

Pattern	Cork cambium cells		Cork cells		
	Dividing cells	Non-dividing cells	Anticlinal division in cork cambium	No anticlinal division in cork cambium	Total surfaces
46	7	13	12	21	53
45	7	21	5	14	47
55	6	8	9	6	29
56	15	3	3	3	24
6	5	7	6	3	21
4664	1	2	8	7	18
5	2	11	.....	3	16
6545	.....	.....	7	7	14
6445	.....	.....	8	4	12
47	9	.....	.....	2	11
654	.....	.....	3	5	8
554	4	3	.....	.....	7
465	3	.....	1	2	6
5555	.....	.....	3	3	6
4555	.....	.....	1	5	6
464	.....	.....	3	2	5
46465	.....	.....	4	1	5
6456	.....	.....	4	.....	4

Six other patterns each occurred 3 times.
Nine other patterns each occurred 2 times.

Table 7 gives the kinds of faces found on the tangential surfaces of cork cambium cells. The preponderant face on both dividing and the non-dividing cork cambium cells is the hexagon. Table 9 gives the types of tangential faces found on the cork cells; the cork cells from undivided cork cambium cells have hexagons as the most frequently occurring face and in cork cells from anticlinally divided cork cambium cells pentagons are most frequent.

Table 13 summarizes the data for the 16 most frequently recurring patterns of faces on the radial surfaces of both the cork and cork cambium cells. The most frequently recurring radial surface pattern in cork cambium was one with 4 faces; a quadrilateral, a hexagon, and 2 pentagons. In the cork cells the radial surface pattern which occurred most often contained 2 faces, a quadrilateral and a hexagon. Of the remaining patterns, which occurred more than once and are not shown in the table, 2 occurred on 3 surfaces and 9 on 2 surfaces.

The patterns of the faces on the top and bottom surfaces are summarized in table 14 which shows the 18 most frequently recurring patterns. That which appeared most often on the top and bottom surfaces of the cork cambium cells, 28 times, consisted of a quadrilateral and a pentagon. In the cork cells the most frequently appearing pattern contained a quadrilateral and a hexagon; this appeared 33 times. Of the patterns which occurred

more than once, and which do not appear on the table, there were 6 patterns which repeated 3 times and 9 patterns which occurred twice.

In the tissues examined, the cork cells were laid down in radial rows by a single cork cambium cell at the end of each row. The cells were studied in sequence as they appeared in a single row. In this way it was possible to see whether the cells from a single cork cambium cell resembled each other. Table 15 shows such a sequence of cork cells which was formed by a cork

TABLE 15. *Patterns on the tangential, radial, and top and bottom surfaces of a series of cork cells derived from a single cork cambium cell. The top cell in the table is nearest the epidermis.*

Top	Bottom	Surfaces of cork cells			
		Front tangential	Rear tangential	Left radial	Right radial
6–4 4–7	5 6 4 4 5	9	8	5–5 4–6	4–6–4
6–4 4–5	7 4 4 5 6	8	8	5–5 4–6	7 4–5–5
5–4 5–6	6–5 4–5	8	8	6–4 4–6	4–6 6–4
5–4 5–6	5–6 5–4	8	8	5–5 5–5	4–6 6–4
4–6 6–4	5–6 5–4	8	8	6–4 4–6	5–5 6–4
4–6 6–4	5–5 5–6	8	8	6–4 5–5	6–5 4–6–4

cambium cell which had not undergone an anticlinal division. An examination of this sequence of cells shows that the pattern of faces on each of the surfaces of succeeding cells is similar, but not identical, in number, arrangement, and kinds of faces.

Discussion. The average dimensions of the cork cambium and the cork cells show that they are elongate cells with the long axis running parallel to the axis of the stem. The cork cambium cells are generally rectangular in transverse section (figs. 1 & 2), the radial dimension being shorter than the tangential. In the cork cells growth occurs in the radial direction, giving them a less flattened appearance in transverse section (fig. 5). This orientation of the cells is not like that found in the common bottle cork, derived from *Quercus suber*. In the latter plant the cork cells are elongated with the long axis of the cell lying at right angles to the axis of the stem; von Mohl (1845), Eames and MacDaniels (1947).

One of the major factors determining the shapes of cells is the presence or absence of divisions in cells contacting the cells being studied. When the data for the number of faces on the dividing cork cambium cells are com-

pared with the data for the number of faces on the non-dividing cells, it is immediately apparent that both the average number of faces per cell and the modal class for this characteristic are significantly higher (as shown by a t test) in the dividing than in the non-dividing cells. Dividing cells had an average of 14.92 faces per cell, and there were more cells with 16 faces per cell than any other number of faces; on the other hand, the average number of faces for the non-dividing cells was 13.46, and the group with 13 faces per cell was the mode. In studying the distribution of dividing cells at any one level in the stem, it was noted that divisions occurred in restricted areas, i.e., not all cork cambium cells at a given level in the stem are undergoing division at the same time. This behavior of dividing cork cambium cells was reported by Sanio (1860) in his researches on the periderm. Since this is so, a dividing cork cambium cell is likely to be adjacent to another dividing cell or a cell that has recently divided. Non-dividing cells, on the other hand, are more likely to be surrounded by other non-dividing cells than by those that are dividing. Divisions in cork cambium are chiefly periclinal, and so an increase in the number of faces would be expected on the radial and top and bottom surfaces of those cells which are in contact with dividing or recently divided cells. An examination of table 7 shows that the number of radial faces on dividing cells was 418 as compared with 376 on non-dividing cells. Similarly, the number of faces on the top and bottom surfaces of dividing cork cambium cells was 222 as compared with 195 for the same surfaces on non-dividing cells. This is, of course, reflected in the average number of radial faces per surface as shown in table 8 where the average for the dividing cells is 8.36 [2.02] faces per surface, and 7.52 [1.45] faces per surface for the non-dividing cells. The average number of faces on the top and bottom surfaces of the dividing cells is 4.44 [1.48] as compared with 3.90 [1.22] for the non-dividing cells. These differences between the averages for the dividing and the non-dividing cells are significant as shown by the t test previously mentioned. Finally, the presence of additional faces on the radial surfaces may be seen in the fact that 43 of the radial surfaces in the dividing cells had 5 or more faces, while only 20 of the radial surfaces on the non-dividing cells had 5 or more faces. This also holds true for the top and bottom surfaces of the dividing and non-dividing cells; 32 of the top and bottom surfaces of the dividing cells had 3 or more faces while only 20 such surfaces on the non-dividing cells had 3 or more faces.

These data would tend to show, then, that the increase in the number of faces on the dividing cell is due in part to recent divisions in neighboring cells. Eventually, the number of faces on the dividing cell would be reduced when it was divided by its own division wall into two daughter cells.

Radial growth also occurs in the cell before it begins to divide. This is shown by the difference (significant according to the t test) between the

radial depths of the dividing and the non-dividing cells. The average radial depth of the dividing cork cambium cells was 25 [5.7] microns while the average radial depth of the non-dividing cork cambium cells was 19 [3.3] microns.

These data would lend support to the idea that radial growth and addition of contacts precede the actual division of the cork cambium cell. This agrees with the results of Matzke (1949) in his work on division of the epidermal cells of the meristem of *Anacharis densa* in which he states that his data indicate that increase in the number of faces occurs mostly before the cell divides.

In his work on the shapes of fusiform cambial initials Dodd (1948) pointed out that, "Radial growth and tangential division affect the shape of the fusiform cambial cell." This is in accord with the data presented here.

The distribution in the number of faces per cell for the non-dividing cork cambium cells shows a bimodal character. The range in the average length of the cells signifies that there is a difference in the size of the cork cambium cells. When the number of contacts is not being increased by the division of neighboring cells, differences in the number of contacts may be due to differences in cell size. In the cork cambium tissue large cells may have neighboring small cells. As shown by Matzke (1939 & 1946) in his studies of lead shot and bubbles, when large and small shot or bubbles are mixed the small shot or bubbles tend to have fewer than 14 faces per cell, and the large shot or bubbles tend to have more than 14 faces per cell. This was also found to be true for cells by Marvin (1944) and Lewis (1944) in their studies of the cell shapes of pith cells in two species of *Eupatorium*. This is possibly the explanation of the bimodal distribution of the number of faces per cell in the non-dividing cork cambium cells, since large and small cells are mixed together in this tissue.

The effect of division on the shape of cells, as expressed by the number of faces, is well demonstrated in the cork cells of this plant. As stated previously, there are two classes of cork cells, one including cork cells which had been formed by a cork cambium cell that had undergone an anticlinal division, and the other group consisting of cells which originated in cork cambium cells which retained the dimensions of the original initial, i.e., no anticlinal divisions had taken place.

The range in the number of faces per cell in the cork cells coming from anticlinally divided cork cambium cells was from 9 to 19, with a distinct modal class at 11 faces per cell. Twenty-four per cent of all the cells in this group had 11 faces per cell. The average number of faces per cell was 13.10.

When these figures are compared with comparable values for the cork cells which came from cork cambium cells which had not undergone an anti-

clinal division, a significant difference (shown by a t test) is noted. The range in the number of faces per cell was 9 to 23; the modal class was at 13, and the average number of faces per cell was 14.72.

The differences in the average number of faces per cell and in the modal class between the two groups was probably due to the anticlinal division which had taken place in the cork cambium cells forming these cork cells.

In his paper on the shape of the cells in elder pith, Lewis (1923) pointed out that when a 14-faceted cell was divided in half, and the plane of division passed through the surface of the faces, the two remaining cells each had 11 faces. The average number of faces for the entire group of cork cells was 13.91 which is close to 14. If the cells did not enlarge and no new contacts were added before division, it is possible that the 11-faceted cork cells arose by the division of 14-faceted cells.

The plane of the anticlinal cell division passes through the tangential surfaces of the cork cambium cell. From table 9 it is seen that in the cork cells which come from an anticlinally undivided cork cambium cell the hexagon is the predominant type of face; 46 of the faces or 46 per cent were hexagons. In the cork cells which came from cork cambium cells which had undergone an anticlinal division pentagons were more numerous than any other type of face on the tangential surfaces: 42 faces or 42 per cent of the total. If a hexagon is divided in half, and the plane of division goes through the sides of the face, 2 pentagons result. The types of faces on the two kinds of cork cells may thus be explained.

A comparison between the cork cells and the cork cambium cells, with regard to the number of faces per cell, shows a stronger resemblance between the non-dividing cork cambium cells and the cork cells, than between the dividing cells and the cork cells. The range in the number of faces per cell on the cork cells was from 9 to 23. If the data are examined more closely, however, it is seen that there was but one cell with 23 faces, the bulk of the cells ranging from 9 to 19 faces per cell. In comparison, the range in the non-dividing cork cambium cells was from 10–17, which is fairly close. The distribution for both the cork cells and the non-dividing cork cambium cells shows a bimodal character, the primary peak in both being at 13 faces per cell, and the secondary peak at 15 faces per cell. In the dividing cork cambium cells the range is from 10 to 20 faces per cell, which is similar to the cork cells, but the modal class is at 16 faces per cell, and furthermore, the curve is unimodal. Further evidence for the similarity between cork cells and non-dividing cork cambium cells is seen by comparing the average number of faces per cell of the two categories. The average number of faces per cell for the cork cells, 13.91, is not significantly different from the 13.46 faces per cell of the non-dividing cork cambium cells. On the other hand, the difference between the average number of faces per

cell on the dividing cork cambium cells, 14.92, is significantly different (as shown by a *t* test) from the average number of faces per cell on the cork cells.

In both the cork and the cork cambium cells pentagons were more numerous than any other type of face; 457 or 32 per cent of the faces were pentagons in cork cambium cells, and 463 or 33 per cent in the cork cells. Quadrilaterals, pentagons, and hexagons accounted for 1175 or 83 per cent of the faces in the cork cambium, and 1300 or 93 per cent of the faces on the cork cells. This is in agreement with the distribution of kinds of faces found on the cells investigated in previous studies. As might be expected, the cork tissue shows greater regularity in this respect than the cork cambium tissue, since division with its resultant effects on the kinds of faces, is not present in this tissue. This regularity in the cork cells is further evinced by the fact that the number of quadrilateral, pentagonal, and hexagonal faces is almost the same, being (in round numbers) 29, 33, and 32 per cent of the total number of faces respectively.

Five lenticular or 2-sided faces were found on the cork cambium cells, appearing between the radial and tangential surfaces of 4 of the cells. These cells were elongate, including the longest cell (fig. 17) and 3 other long cells. This type of face was reported in the literature by Dodd (1948) as occurring on the lateral and tangential surfaces of fusiform cambium initials in the stem of *Pinus sylvestris*. As in that tissue, the lenticular faces occur in cork cambium cells at a point where 4 cells come together in a section, a 4-rayed vertex. As suggested by Dodd these 2-sided faces may be due to curvatures in the tangential face which cause it to cross and recross a radial face. Another similarity between the cork cambium cells and the cambial cells mentioned above is that triangular faces are found in significant numbers in both tissues. In the cork cambium cells 72 or 5 per cent of the faces were triangular (fig. 25). This is not so great a number as the 13 per cent found by Dodd, but it is far greater than the number found in undifferentiated cells.

Most of the faces in both the cork and cork cambium cells met in a stable trihedral angle. One tetrahedral angle was found in the cork cambium cells and 3 were found in the cork cells (fig. 38). Although the number of such angles found in the cork cells was greater than the number found in the cork cambium cells, their frequency does not approach the figure obtained by Lewis (1928) for cells of commercial cork. In that study he stated "That this average is not precisely 14 is due to the frequent elimination of a surface accompanying the production of a tetrahedral angle. The computation indicates that 40 per cent of the cells have lost a side in this way."

When the shape of cork cambium cells is studied from the aspect of the number of different combinations of faces which exist on the cells, it is

readily seen that the tissue is heterogeneous. There were 86 different combinations of faces in the 100 cells studied. No one combination occurred more than 3 times, and in this latter group there were only 2 combinations.

The cork tissue was more homogeneous as expressed by the number of combinations of faces found on the cells. There were 55 different combinations of faces in the 100 cork cells. Fifteen of these combinations occurred more than once; one of them occurred 9 times, one of them 8 times, and others in decreasing frequency. The 8 most frequently occurring combinations for both the cork and cork cambium cells are recorded in table 5.

A greater number of combinations was found by Matzke (1949) in the parent cells than in the daughter cells of epidermal meristem cells in *Anacharis densa*. This is in agreement with the results of the present study, where the cork cambium cells, the cells in which active division occurs, have a greater number of combinations of faces than the cork cells derived from them. As stated by Matzke in the paper cited above, this may be taken as evidence to support the thesis that changes occur before and during division rather than after division has taken place.

One of the two combinations which occurred 9 times included cells with 14 faces. A study of the arrangements of the faces from conventional models shows that this combination existed in 3 different arrangements. Table 6 gives an analysis of the kinds of faces found on each of the surfaces in this 4–4–6 combination.

In his long series of papers on cell shapes, Lewis has postulated that the orthic tetrakaidecahedron is the basic geometrical solid upon which the shape of all cells is based. In this investigation of 200 cells, 100 cork and 100 cork cambium, no cell was found which had only the 6 quadrilaterals and 8 hexagons of the orthic tetrakaidecahedron. The great variability in the forces determining the shapes of cells precludes the finding of many actual cells with this configuration of faces. Approaches and approximations to this figure have been found in the cells which have been studied in this investigation. The 9 cork cells, with the 4–4–6 combination, analyzed in table 6, may be classified with this group of "near misses." These 9 particular cork cells are more similar to an orthic tetrakaidecahedron than to any other regular or semi-regular geometric figure.

Seven of the 9 cells in the 3–6–2 combination were cork cells which were derived from a cork cambium cell which had undergone an anticlinal division; the remaining 2 were cork cambium cells. The tangential surfaces of these cells were all pentagons. From table 7 it can be seen that hexagons are the most common type of face on the tangential walls of the cork cambium cells. A division through the sides of these hexagons, as in the anticlinal division in the cork cambium cells, would produce 2 pentagons. From the data at hand one cannot say with certainty that these 11-faceted cells

were derived from an original cell with 14 faces, but this remains as a distinct possibility.

In the 8 most frequently occurring combinations there were 50 cells, consisting of 38 cork cells and 12 cork cambium cells. These 50 cells had their faces arranged in 20 different ways. This figure would tend to indicate that the cells of this group are not particularly homogeneous since these cells are the most similar of the entire group so far as the number of faces per cell is concerned, yet their faces are arranged in 20 different ways.

A comparison of the frequency of occurrence of the most commonly found combinations of faces on the cork and cork cambium cells with the frequency of the same combination of faces on the cells and bubbles previously studied is made in table 16. It can be seen that these combinations

TABLE 16. *Frequency of the most common cork and cork cambium combinations of faces in various previously studied cells and bubbles.*

Type of cell or bubble	No. of cells or bubbles	Combinations of faces				
		4–4–6	3–6–2	4–4–4	2–8–3	5–4–4–2
Eupatorium purpureum pith (Marvin 1939)	100	3	3	3	1	.....
Angiopteris petiole (Higinbotham 1942)	100	.....	3	.....	1	.....
Citrus grandis-carpel vesicles (Dodd 1944)	100	.....	.....	2	2	2
Ailanthus pith (Hulbary 1944)	150	6	3	6	.....	.....
Elodea cortical cells (Hulbary 1944)	600	.....	1	5	2	.....
Peripheral bubbles (Matzke 1946)	400	.....	67	9	5	.....
Central bubbles (Matzke 1946)	600	12	2	1	19	.....
Small bubbles (Matzke and Nestler 1946)	150	1	8	4	4	.....
Aloe aristata epidermis (Matzke 1947)	200	.....	34	.....	2	.....
Elodea meristem epidermis (Matzke 1948)	200	.....	14	.....	.....	.....
Asparagus root parenchyma (Hulbary 1948)	100	6	.....	6	.....	1
Rhoeo leaf parenchyma (Hulbary 1948)	100	5	1	8	.....	.....
Utricularia-internal cells	600	.....	12	.....	.....	.....
epidermal cells (Flint 1949)	300	.....	14	.....	.....	.....
Elodea meristem-epidermis-parent	100	.....	8	1	.....	.....
daughter (Matzke 1949)	200	.....	9	.....	.....	.....
Totals	4000	33	179	45	36	3
Cork cells	100	9	7	8	.....	.....
Cork cambium cells	100	.....	2	.....	3	3
Totals	200	9	9	8	3	3

of faces are not peculiar to the cork and cork cambium cells here studied, but that they occur in other cells and in bubbles.

The significance of the mirror image pairs is not evident. Although one pair of the 3–6–2 combination of cells came from a pair of cork cambium cells which were formed by an anticlinal division from a single cell, their faces, in the tissue, were not oriented in the mirror image arrangement (figs. 32 & 35); neither were the cells adjacent to one another. None of the members of the other mirror image pairs was adjacent to each other in the tissue.

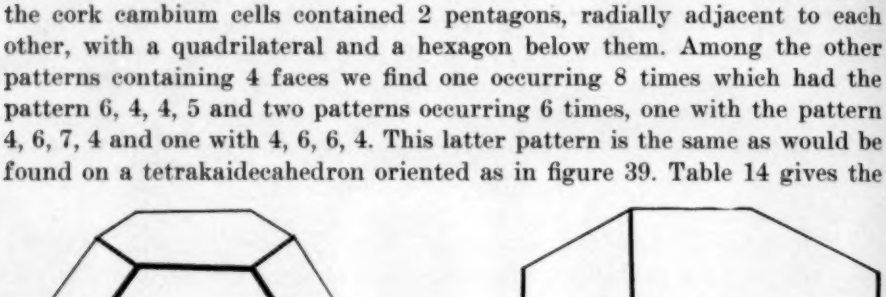
It is possible to construct a hypothetical average cork cambium cell from the data collected in this investigation, but it must be emphasized that this hypothetical average cell never appeared in the tissue.

If we deal first with the average figures for the number of faces on each surface of the cork cambium cell, table 8 furnishes the necessary data. When the figures for the number of faces on each surface are rounded off we obtain 1 face for each of the 2 tangential surfaces, 8 faces for the 2 radial surfaces or 4 faces per surface, and 4 faces for the top and bottom surfaces or 2 faces each for top or bottom. This average cell would thus have a total of 14 faces. This average cell may be constructed from another set of data, those shown in table 11, where the actual distribution of the number of faces per surface is given. The modal class for the tangential surface is unquestionably 1 face per surface, for each radial surface 4 faces, and for the top and bottom surfaces 2 faces each. This again gives a cell of 14 faces.

The average cambium cell postulated by Dodd (1948) can be reconciled with the average cork cambium cell derived here. In his average cambium cell, he had 18 faces; 4 of these, however, are ray contacts which do not appear in cork cambium tissue. This lowers the average to 14, the same as found for the average cork cambium cell. The tangential faces on the cambium cell had an average of 10 sides, but removing the ray contacts lowered the figure to 6 sides; as shown by the data, hexagons were the most common type of tangential face found in the cork cambium cells. The 12 lateral faces, 6 on each radial surface of the average cambium cell, might be interpreted as the 4 radial faces of the cork cambium cell plus the 2 bottom faces on the one radial surface, and the 4 radial faces plus the 2 top faces on the other radial surface of the cell. Thus it is possible to draw a fairly close comparison between the average cells of these two lateral meristem tissues.

An attempt may be made to determine the kinds of faces on this hypothetical average cell by analyzing the frequency with which certain combinations of faces occurred on the various surfaces in the actual cells. Table 13 gives the frequency of occurrence of the 16 most common patterns on the radial faces of the cork cambium cells. Since the average cork cambium

cell had 4 faces per radial surface, a pattern should be chosen with that number of faces. The 4-faceted pattern which occurred most frequently in the cork cambium cells contained 2 pentagons, radially adjacent to each other, with a quadrilateral and a hexagon below them. Among the other patterns containing 4 faces we find one occurring 8 times which had the pattern 6, 4, 4, 5 and two patterns occurring 6 times, one with the pattern 4, 6, 7, 4 and one with 4, 6, 6, 4. This latter pattern is the same as would be found on a tetrakaidecahedron oriented as in figure 39. Table 14 gives the



39

FIG. 39. This illustration shows an orthic tetrakaidecahedron in 2 views. The drawing on the left shows the figure oriented in the same manner as a cork or cork cambium cell when viewed from a tangential surface. The hexagon of this surface is bordered by the 2 radial, the top, and the bottom surfaces. The drawing on the right shows the figure viewed from a radial surface. The 4 faces of this surface show the 4, 6, 6, 4 pattern found on the radial surfaces of some of the cells. In this same drawing the bottom surface presents the 4, 6 pattern found on some of the cells.

frequency of occurrence of the 18 most common patterns of faces in the top and bottom surfaces. In the cork cambium cells the pattern consisting of a quadrilateral and a pentagon occurred most often. Table 7 gives the frequency of the different types of tangential faces; the one which is most common in all cork cambium cells is the hexagon. Difficulty arises when an attempt is made to put this average cell together since the arrangement and kinds of faces for the respective surfaces will not fit together to form a cell. This is one of the pitfalls of dealing in hypothetical averages. Even in attempting to construct an average cell there is difficulty in finding one which can be called typical of the tissue being studied. Hence, it is possible only to say that an average cell would have a configuration of faces on certain surfaces which resemble those found on an orthic tetrakaidecahedron.

In his paper on the shape of the tracheid in pine, Lewis (1935) reports that because of the tangential divisions in the cambial cells the tracheids are oriented with an edge rather than a face on the upper and lower sur-

faces of the cells. This is in accord with the orientation in the cork cambium (figs. 18 & 20–27) and cork cells (figs. 28, 29, 31–34 & 36–38) where 2 faces of the top and bottom surfaces met in an edge rather than having a single face for the top and bottom surfaces.

No attempt has been made to derive an average cork cell for this tissue since it may be that an interpretation of the shapes of these cells is best accomplished by taking into account the position of the walls of adjacent cells.

The shape of any single cork cell is determined by the relative positions of the surfaces of its neighboring cells. The data in tables 9 to 12 show that there are 6 categories of cork cells, depending, first, upon whether they come from a cork cambium cell which has divided anticlinally or not, and then upon the position of the radial walls of the cells above or below the cell being studied, i.e., the radial surface may cut across neither top nor bottom surface, may cut across one but not both, or may cut across both the top and the bottom.

The averages for each of the surfaces of all the cork cells are given in table 10. The average number of tangential surfaces is 2 per cell or one for each surface. The average number of radial faces per cell is 6, or 3 for each surface. There is an average of 6 faces for the top and bottom surfaces of the cell or 3 faces for each surface, top or bottom. This would give a cell with 14 faces, but if table 11 is consulted it is seen that the occurrence of the 3-faceted radial, and top and bottom surfaces is not very frequent. The greatest number of radial surfaces had 2 faces per surface with a secondary maximum at 4 faces per surface. A similar situation exists for the distribution of faces on the top and bottom surfaces. Because of the non-agreement of these data it is felt that the construction of an average cork cell would be of little value in interpreting the shapes of these cork cells.

When the shapes of the cork cambium cells are compared with the shapes of the cork cells presented in this study it is evident that differences exist between the two types. This may be interpreted as being due to two factors. First, the cork cells and the cork cambium cells did not come from the same piece of tissue. As mentioned previously, cork tissue is variable from sample to sample. The second factor, and probably more important, is that both the dividing and the non-dividing cork cambium cells were chosen soon after they had been formed because of difficulties in identifying non-dividing cork cambium cells in older tissue. None of these cork cambium cells had undergone an anticlinal division. A close correspondence may well exist between a cork cambium cell and the cork cells directly derived from it.

The data given by Lewis (1928) for cells in commercial cork agree with the data for the cork cells in *Pelargonium* in certain respects only. The average number of faces per cell given by him is 13.60, which agrees fairly well

with the average of 13.91 for the cork cells in this investigation. The cork cells, however, are taken from different plants in the two studies, and the method of investigation is different in each case. Further, the orientation of the axes of the two kinds of cells with respect to the stem is not the same; in *Pelargonium* the long axis of the cork cells is parallel to the axis of the stem and in commercial cork the long axis of the cells is at right angles to the axis of the stem.

The sequence of cells enumerated in table 15 shows that the daughter cells from a single cork cambium cell resemble each other both as to the kinds and arrangements of faces. This repetition of pattern was noted in many series of cork cells and brings to mind the statement of Hooke (1665) that the cells are, "not very deep, but consist of a great many little boxes separated out of one continued long pore by certain diaphragms." Hooke's "one continued long pore" would be the series of cells formed by a single cork cambium cell. These data tend to show that his "many little boxes" have similar surfaces.

SUMMARY

1. The three-dimensional shapes of 100 cork cambium and 100 cork cells from the stem of *Pelargonium hortorum* Bailey were reconstructed for the purpose of making a comparison between lateral meristem cells and the cells produced by them. A comparison was also made between dividing and non-dividing cork cambium cells.

2. Measurements of the cork cambium cells show them to be elongate in a direction parallel to the axis of the plant and to have a rectangular outline in cross-section, with a shorter radial than tangential dimension. Cork cells were similarly elongate, but had the radial dimension larger than that of the cork cambium cells.

3. Dividing cork cambium cells had a higher average number of faces per cell (14.92) than non-dividing cells (13.46) presumably due, at least in part, to the greater number of adjacent dividing cells in the former group.

4. The data tended to demonstrate that the increase in the number of faces per cell preceded the actual division of the cell.

5. In the material analyzed, the cork cells were of two general kinds, one produced by cork cambium cells that had undergone an anticlinal division, and the second, cork cells that came from a cork cambium cell that had not undergone such a division. The average number of faces per cell for the former group was 13.10, while the average for the latter was 14.72 faces per cell.

6. Non-dividing cork cambium cells resembled cork cells more closely than they did dividing cork cambium cells.

7. Pentagonal faces occurred most frequently in both the cork and cork cambium cells; quadrilaterals came next in frequency in the cork cambium

cells, followed by hexagons; in the cork cells hexagons came second with quadrilaterals third.

8. There were 86 different combinations of faces in the cork cambium cells and 55 combinations in the cork cells. Cork cells were more homogeneous in this respect and had two combinations which occurred 9 times, consisting of 4 quadrilaterals, 4 pentagons, and 6 hexagons (4–4–6), and 3 quadrilaterals, 6 pentagons, and 2 hexagons (3–6–2). In the cork cambium cells the two most frequently occurring combinations appeared 3 times and contained 5 quadrilaterals, 4 pentagons, 4 hexagons, and 2 heptagons (5–4–4–2), and 2 quadrilaterals, 8 pentagons, and 3 hexagons (2–8–3).

9. An average cork cambium cell could logically be reconstructed from the data. This hypothetical average cell had 14 faces distributed as follows: 1 face for each of 2 tangential surfaces, 4 faces each for 2 radial surfaces, and 2 faces each for the top and bottom surface.

10. Many aspects of the shapes of the cork cells could be explained in terms of the divisions which occurred in the cork cambium cells producing these cells, and by the positions of the radial surfaces of the cells above and below the cork cells being studied.

11. A serial sequence of the cork cells produced by a single cork cambium cell showed that the cells in such a sequence were similar but not identical to one another both with respect to the kinds of faces and to the arrangements of those faces.

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THE MORPHOLOGY AND CYTOLOGY OF LEMANEA AUSTRALIS ATK.[1]

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A great local abundance of large colonies of *Lemanea australis* Atk., together with the paucity of detailed knowledge of this reputedly primitive genus of Rhodophyceae, suggested that a morphological and cytological investigation of this alga might be fruitful, despite the fact that Kylin (1923) had asserted, "*Lemanea* ist gar kein günstiges Objekt für zytologische Untersuchungen." A survey of pertinent literature showed an obvious need for such a study. Drew-Baker (1944) had explicitly stated in her review of the nuclear and somatic phases in the Florideae, "no cytological work has been done on the . . . Lemaneaceae." Hence this study was undertaken in an attempt to fill that gap.

According to the classification of the Florideae proposed by Kylin (1928, 1937) and accepted by Fritsch (1945a) and most other workers, the Lemaneaceae is one of eight well-defined families of the order Nemalionales. This order comprises about 250 species, and is agreed to be the most primitive of all the Florideae, although its genera manifest considerable variability in cystocarp structure and types of life history. As a rule, tetraspores are not produced, and meiosis is presumed to occur in the zygote, but evidence for the latter opinion is scanty. Svedelius (1915) first demonstrated zygotic meiosis in a member of the Nemalionales when he observed the presence of diakinetic chromosomes in the first division of the zygote nucleus of *Scinaia furcellata* (Turn.) Bivona of the Chaetangiaceae. This evidence was soon strengthened by Kylin's (1916) study of *Nemalion multifidum* (Web. & Mohr)J. Ag., in which diakinesis was again shown to occur in the carpogonium. Kylin's (1917a) work on *Batrachospermum moniliforme* Roth. and Cleland's (1919) prophase figures of the zygotic division in *Nemalion multifidum* were further grounds for a general acceptance of the prevalence of zygotic meiosis in the Nemalionales. Svedelius (1933) reported meiosis in *Asparagopsis armata* Harv. and *Bonnemaisonia asparagoides* (Woodw.) Ag. but, as Drew-Baker (1944) has noted, the evidence for this is not convincing. Several genera of the Nemalionales are known to produce tetraspores; among these are *Rhodochorton violaceum* (Kütz.) Drew-Baker, *Liagora tetrasporifera* Boerges and *Helminthocladia Hudsonia* (C. Ag.)

[1] Portion of a thesis submitted to the Faculty of the Graduate School of Vanderbilt University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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J. Ag. In view of the fact that meiosis universally occurs in the tetrasporangium of all diplobiontic Florideae, it is not at all unlikely that these forms will eventually be shown to have a postponement of the reduction division. Thus far, there is no cytological evidence of this in the literature.

Bory first described the genus *Lemanea* in 1808 (Palmer 1941), but he included in it several species of *Batrachospermum*. In 1828 C. A. Agardh (Palmer 1941) revised the genus to its present status. Sirodot (1872) was the first to devote extensive attention to the family Lemaneaceae. His work was based on a surprisingly competent knowledge of the gross morphology of these plants. He discovered the organs of reproduction, recognized the basic structural units of the sexual shoot, and saw the relationship existing between the Chantransia-stage and the mature thalli. The publication of his work corrected the errors of earlier investigators, all of whom had been unable to follow the complete life-cycle of the plant. Sirodot also showed that there are two well-defined groups in the family, and he gave these groups generic rank: to those plants whose axial cells lack entwining hyphae he gave the generic name *Sacheria*, while he retained *Lemanea* (Bory) Agardh for those whose ray cells produce enveloping filaments that surround the central axis.

Atkinson (1890)[2] gave these two genera of Sirodot only subgeneric rank in his monograph of the Lemaneaceae of the United States. This practice is maintained at the present time. Atkinson not only reduced the rank of the two groups, but, in addition, included several species of European *Sacheria* in species most common in America, namely, *Lemanea* (*Sacheria*) *fucina* Bory and *Lemanea* (*Sacheria*) *fluviatilis* Ag. Palmer (1945) has questioned the wisdom of this latter change. In his study of the second subgenus, *Eulemanea*, Atkinson (1931) added three new species, and thus increased the number of American species to eight. These are: *L. annulata* Kütz., *L. australis* Atk., *L. catenata* Kütz., *L. grandis* (Wolle) Atk., *L. mexicana* Kütz., *L. nodosa* Kütz., *L. pleocarpa* Atk. and *L. torulosa* Sirodot.

Kylin (1923) has reported the result of a brief study of the morphology of *Lemanea* (*Sacheria*) *fluviatilis*. While this complements Atkinson's more thorough work on *Lemanea australis*, it has added very little to our knowledge of the cytology of these plants.

Rosenberg (1935) has reported germination of the carpospores of *Lemanea torulosa* in laboratory cultures.

Finally, Palmer (1941) has made a special study of the distribution of *Lemanea* in North America. He has also published notes on herbarium specimens of *Lemanea* (1942), and on two species that occur in the state of Tennessee (1943).

[2] Atkinson's monograph (1890) is referred to so frequently in this paper, that subsequent citations have been omitted to avoid needless repetition.

Materials and methods. While collections were made from several localities in the Nashville region, all of the plants[3] used in this investigation were obtained from an area of about fifty square yards in Richland Creek near Nashville. The plants were collected at different hours of the day and night, on an average of once every two weeks for a period of two and a half years. The material was invariably fixed in the field or within an hour after collection.

Microscopic examination of living plants was continued throughout the period of study as an aid to the interpretation of fixed and stained material. No extensive attempts were made to cultivate the plants in the laboratory, due to the ready accessibility of an unlimited supply of fresh material. Spore germination and early phases in development of the Chantransia-stage and sexual shoots were studied in laboratory cultures in "Volvox" solution (Moewus 1940).

Fifteen standard fixatives were used, as well as modifications of some of them. In general, it was noted that all of these fixatives were more satisfactory when they were warmed to 50° C., and when the material was maintained in the fixative at that temperature for about twenty minutes, with a total fixation time of about twelve hours. The fixative that yielded the most consistently good results was Allen's B-15 mixture. The material was left in this fixative for about twelve hours, and then placed in 70% alcohol and washed until all the picric acid had been removed. Dehydration and clearing were accomplished in a graded series of ethyl alcohol and xylol. The material was embedded in paraffin with a melting point of 53° C., and sectioned serially at 6 to 10 μ.

A great variety of stains was used; Heidenhain's haematoxylin, counterstained with Fast Green, was far superior to others, but it had the disadvantage of staining the prominent pit-connections and certain ergastic substances as deeply as it did the chromatin. The standard Feulgen technique was used in supplementary fashion, therefore, in order to avoid misinterpretation, and this objective was achieved, although the material is frequently only faintly Feulgen-positive.

The drawings were made with a Zeiss Lumipan and camera lucida at table level. Field pictures were made with a Kine Exakta camera equipped with a Zeiss biotar lens and extension tubes. Photomicrographs were taken with a Leitz Micam camera.

Observations. Habitat. *Lemanea* is a lithophilic benthophyte. In the region of Nashville it is confined to limestone rocks which form the bedrock of the fresh-water streams of the region. The plants are aggregated and

[3] The plants used in this investigation differ from typical *L. australis* Atk. in their possession of chantransial filaments of uniform diameter. They are currently being studied by Dr. C. M. Palmer, who expects to publish his opinion as to their proper taxonomic disposition.

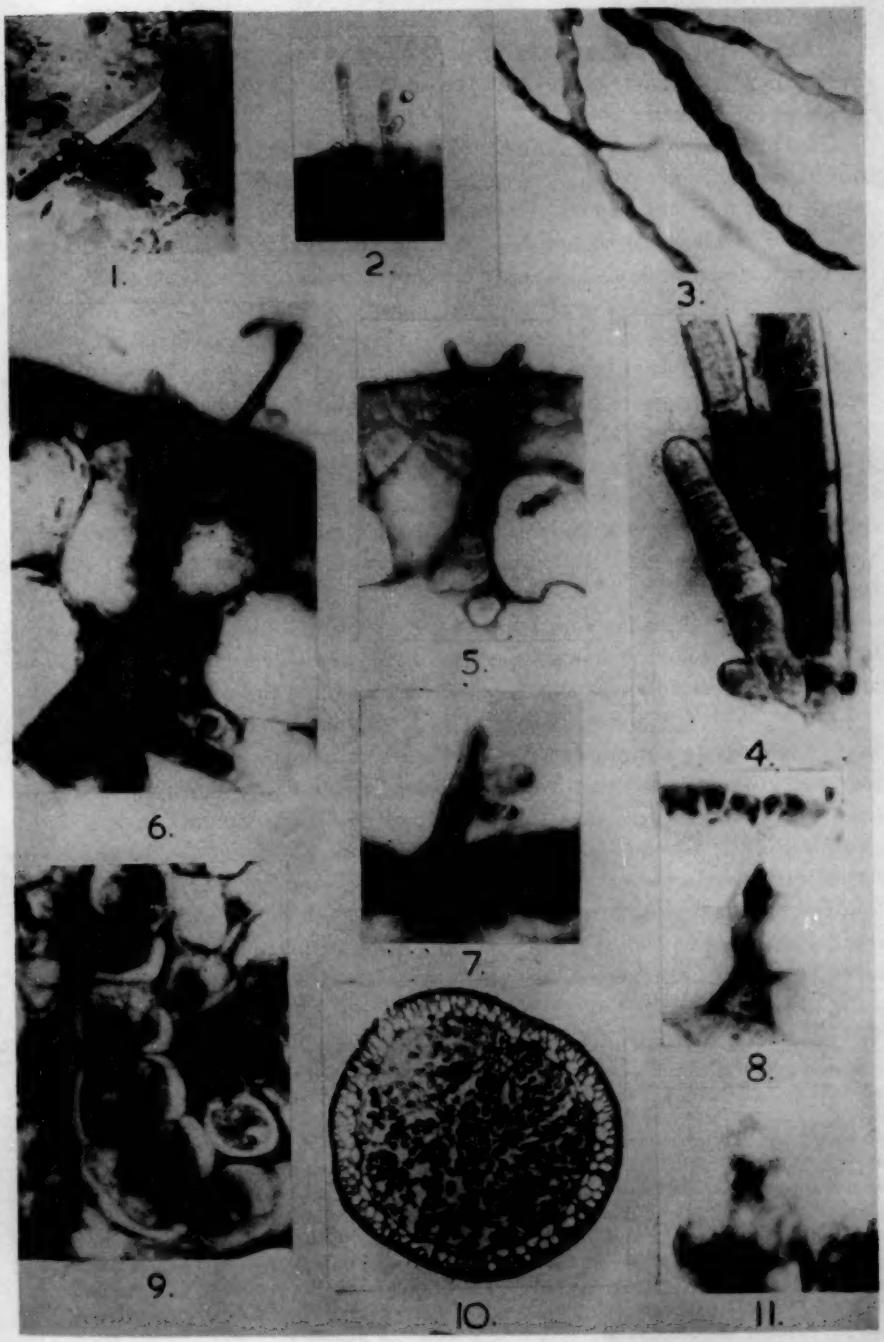
form large olive- to blackish-green carpets on the downstream surface of the rocks. At the very edge of these rocks, the sexual shoots usually develop earlier in the year, and grow to greater lengths than do the plants which are confined to the middle of the rocks. This is probably because that particular location provides the prostrate perennial plants with a more abundant and persistent supply of water when they are ready to produce the Chantransia-stage. In the Nashville region the plants are confined to Ordovician limestone bedrock; they never occur in streams where the bottom is made up of gravel.

The hydrogen ion concentration as well as the presence or absence of one or more salts in the stream may well be critical factors affecting the presence or absence of the alga in a locality. In that part of Richland Creek in which the plants used in this study were growing, the pH value of the water was determined to lie usually between 7.5 and 8.0. This falls well within the range of Shoup's (1947, 1950) reports on water analyses of the streams of Middle Tennessee.

Shade provided by overhanging trees appears to be an important factor in determining the presence or absence of *Lemanea* in the streams in which the substrate is suitable. The plants are rarely found in a habitat that is not shaded for a considerable part of the day. The Chantransia-stage is frequently associated with a plentiful cover of fallen leaves and other organic debris.

Temperature range in the life-cycle of *Lemanea* is remarkably wide. Germination of the carpospores, production of the Chantransia-stage and growth of the sexual shoots occur only in the coldest part of the year in the vicinity of Nashville. It was frequently necessary to remove ice from the stream surface in order to collect these stages of the life-cycle. On the other hand, the prostrate form of the plant survives the complete drying of the creek bed and the very high temperatures of summer, and in the late fall it again gives rise to the Chantransia-stage at about the same time that the carpospores, formed the preceding spring, begin to germinate.

FIGS. 1–11. Photographs and photomicrographs of *Lemanea australis* Atk. FIG. 1. Prostrate form on the bare rocks of Richland Creek in midsummer. The darker colonies are Myxophyceae. ×½. FIG. 2. Chantransial filaments projecting through the thallus wall, as a result of intra-thallus germination. ×200. FIG. 3. Detail of sexual shoot. Natural size. FIG. 4. Young sexual shoot on filament of Chantransia-stage. Note unilateral branching. ×400. FIG. 5. Bifurcated trichogyne just prior to fertilization. Note position of egg nucleus. ×300. FIG. 6. Fertilized trichogyne with empty spermatial wall still attached. Note nurse cell at tip of sterile lateral branch at lower right. ×300. FIG. 7. Two spermatia attached to arm of trichogyne. Note two nuclei in the lower spermatium. ×750. FIG. 8. Spermatial nucleus directly above egg nucleus in the base of the carpogonium. Note the advanced disintegration of the trichogyne. ×300. FIG. 9. Chain of migrating nuclei and cytoplasm in gonimoblast. Note displaced pit-connections. ×410. FIG. 10. Transverse section of mature sexual shoot, showing distribution of carpospores, axis cell, spiral filaments, and sterile paraphyses. ×400. FIG. 11. Apical gonimoblast cell in metaphase of mitosis; note the two centrosomes. ×925.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General morphology. Atkinson rightly distinguished three distinct successional forms in the annual cycle of *Lemanea:* these are the prostrate form, the Chantransia-stage and the sexual shoot. They will be described in the order named.

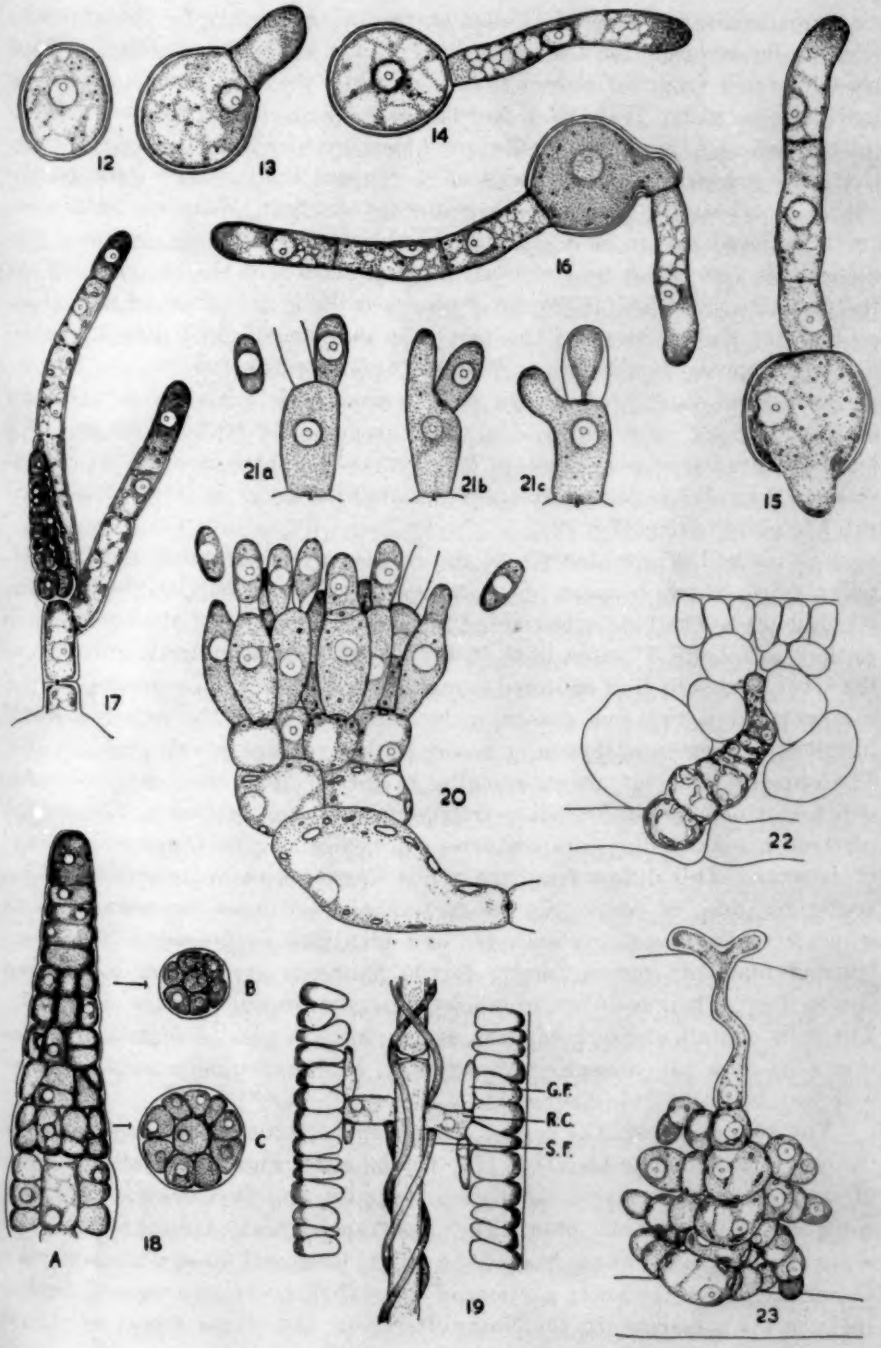
The prostrate form. Lemanea exhibits the heterotrichous habit of growth to which Fritsch (1945b) has attached considerable evolutionary significance. This habit of growth, common to the juvenile stages of the less specialized Florideae, is completely lacking in the Ceramiales. In *Lemanea* the prostrate form is an irregular mass of compacted filaments and densely packed polyhedral cells, which adhere closely to the rock surfaces on which the plant grows. Figure 1 is a picture of these prostrate forms as they occur on the bedrock of Richland Creek in midsummer.

After it is produced by the somewhat retarded growth of a rhizoidal filament from the carpospore (figs. 15 & 16), and increased by the addition of basal rhizoidal outgrowths from the Chantransia-stage and sexual shoots, the prostrate form persists from year to year. Even after several months of severe summer desiccation, it is still able to produce the Chantransia-stage. This has been verified repeatedly by observation of particular prostrate forms *in situ.*

The cells of the prostrate form are thick walled, and the mass has a yellowish-brown color. Various species of Myxophyceae are usually intermingled with its polyhedral cells, as are also numerous diatoms.

The Chantransia-stage. In the late autumn and early winter, when there has been an abundant rainfall, the creek beds become filled with rushing water whose temperature approaches the freezing point, and it is at this time that the prostrate form produces the Chantransia-stage in great abundance. This second successional stage in the life-cycle of *Lemanea* is an important taxonomic criterion in the identification of plants closely allied to *Lemanea australis,* but to collect it is unusually difficult, because of its small size and the depth of the dashing waters in which it grows. The filaments of the Chantransia-stage seldom reach a length of 5 mm. and are only 30 to 40 μ in diameter.

FIGS. 12–23. Camera lucida drawings of *Lemanea australis.* FIG. 12. Mature carpospore. ×410. FIG. 13. Early germination of carpospore. ×410. FIG. 14. Formation of chantransial initial. ×410. FIG. 15. Chantransial filament and early rhizoidal initial. ×410. FIG. 16. Later stage in germination of carpospore. ×410. FIG. 17. Chantransia-stage with young sexual shoot branching laterally. ×200. FIG. 18. Detail of tip of sexual shoot. ×410. FIG. 19. Longitudinal section of stained specimen of young sexual shoot which shows generative filament initial (G.F.), young ray cells (R.C.) and the spiral filaments (S.F.). ×410. FIG. 20. Group of living spermatangia at the tip of a generative filament; the spermatia are in various stages of liberation. ×1225. FIG. 21. Spermatia in various stages of production in living spermatangia. ×1225. FIG. 22. Young carpogonial branch showing the trichogyne, penetrating the cortex of the thallus. ×410. FIG. 23. Mature carpogonial branch with full complement of sterile lateral cells, just before fertilization. ×410.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The Chantransia-stage may also be produced directly by the germination of the carpospores; this may occur either after the carpospores have been liberated from the parent thallus or while they yet remain within its cartilaginous walls. This latter fact has occasioned much misunderstanding in the past, as Atkinson notes. Figure 2 shows young chantransial filaments that have grown through the wall of the parent thallus after germinating within it; this is a frequent phenomenon. At first, Vaucher (Atkinson, 1890) believed this to be a case of reproduction by budding; he later corrected this view when he observed the germination of the carpospores for the first time. Sirodot (1872) never observed the germination of the carpospores, but rightly stressed the fact that the sexual shoot does not arise directly from the carpospore as Vaucher had once asserted.

The carpospores of *Lemanea* show considerable variation in size and shape. They are generally ovoidal or ellipsoidal and between 35 and 45 μ long. Mature carpospores possess a two-layered gelatinous wall, which encloses a granular yellowish-green cytoplasm; the latter is fairly dense just prior to germination (fig. 12).

The method of germination of the carpospore of *Lemanea* is of the bipolar type, which is more characteristic of the Ceramiales than of the Nemalionales. The filaments emerge from opposite poles of the carpospores as they germinate. Figures 13 to 16 are all taken from material cultured in the laboratory, but that collected in nature is similar in all respects. One of the germ tubes, that one slower in development, forms the prostrate form initial after it emerges through a fissure in the carpospore wall (figs. 15, 16). The opposite filament grows apically, to form a long thin chain of cells, which may or may not branch as it extends above the substrate. The clumps of these monaxial filaments comprise the typical sterile Chantransia-stage of *Lemanea*. This differs from the genus *Chantransia* in its lack of monosporangia, and, of course, in the fact that it produces the sexual shoots which are most commonly collected and identified as *Lemanea*. The chantransial filaments remain short; fertile filaments are seldom more than 5 mm. long. Their cells are uninucleated and thin-walled (figs. 15 to 17). The cells contain dense cytoplasm and numerous plastid segments; adjacent cells show pit-connections clearly (fig. 17).Branching is rather sparse, and may be unilateral or alternate.

The sexual shoot. The sexual shoots arise as lateral branches from the chantransial filaments (figs. 4 & 17). These figures illustrate a detailed view of their origin. The sexual shoot grows rapidly, and soon becomes the most conspicuous part of the plant. The chantransial filaments subtending the sexual shoots persist at the base of the latter. Rhizoidal filaments grow down secondarily from the lower portions of the sexual shoots, and serve to anchor them to the substrate. In the Nashville region, the sexual shoots were first

observed in early December, and reached the peak of their development by early March, at which time some few specimens attained a maximum length of 30 cms.

The sexual shoot grows apically (figs. 4, 17 & 18). The single, prominent, dome-shaped apical cell cuts off tabular cells in regular succession as it divides transversely. These tabular cells are broader than long, and form the basic structural units of the adult sexual shoot. Figure 18 represents the growing tip of a sexual shoot in the living condition. Sirodot (1872) and Atkinson correctly interpreted the structural unit of the sexual shoot as consisting of a carpogenic zone with half of each adjoining spermatangial zone. Figure 3 illustrates enlarged portions of mature sexual shoots which are composed of structures resembling the nodes and internodes of higher plants. That this resemblance is merely superficial, is clearly confirmed by careful study of the ontogeny of the shoot.

Figures 18 A, B and C reveal that the tabular cells give rise by periclinal divisions to an axial cell and four or more pericentral cells. The pericentral cells eventually develop into a three to five cell layered mass of pseudo-parenchymatous tissue by further periclinal and anticlinal divisions, while the axial cell merely elongates. This is shown in the lowermost portion of figure 18, which is drawn in sectional view. Atkinson has not explicitly said so, but it is quite certain that the axial cells give rise to the four cruciately arranged ray cells which bear the generative filaments. Figure 19 is taken from a stained specimen, and it proves that this is the case, as examination of the haematoxylin-positive pit-connections indicates. The ray cells remain in contact with the cortical cells by means of clavate tie-cells. Figure 19 represents a longitudinal section of a young "internode" at the level of the generative filament initial. It is clear from this figure that four generative filaments arise from two oppositely situated ray cells. In serial transverse sections of the thallus it can be seen that one of the generative filaments branches soon after it departs from the ray cell. The ray cells always arise from the axial cells near their upper extremities. The spiral filaments, which characteristically envelop the central axis of all species of the subgenus *Eulemanea*, arise only from the lower surface of the ray cells. Figure 19 shows two of these ray cells giving rise to the spiral filaments. Atkinson first used the term "generative filaments" for the "tubes lateraux" of Sirodot (1872). This was a very appropriate change in terminology, for the carpogonial branches originate from the sides of these filaments, while the spermatangia arise from their tips. A more detailed description of these reproductive structures follows.

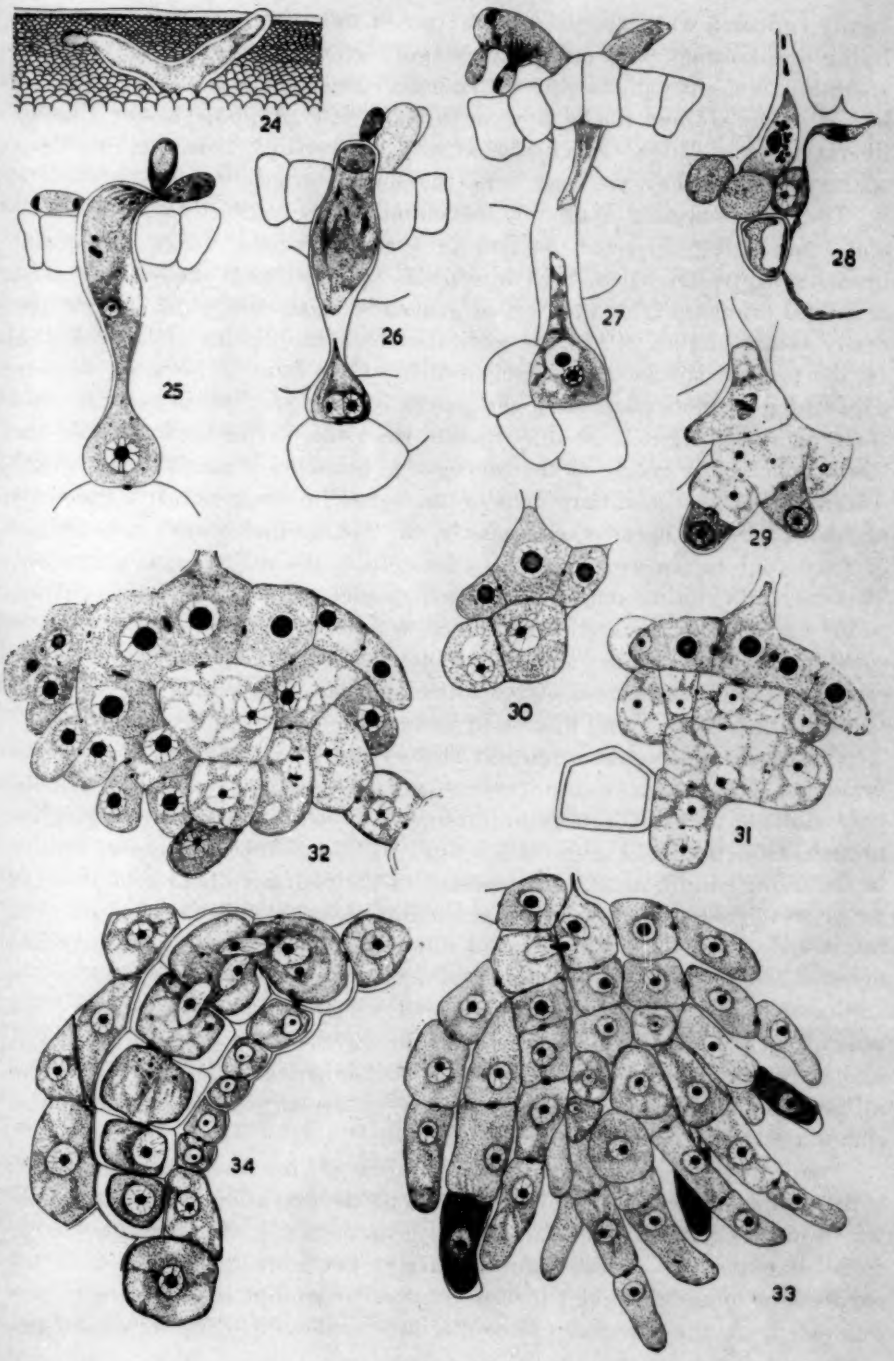
Morphology of reproduction. The male organs. The spermatangia of *Lemanea* are cylindrical unicellular structures which produce a single male cell, the spermatium. The spermatangia are closely packed together, and

arise from ovoid, cortex-like cells which terminate the generative filaments. Their arrangement into variously shaped groups or patches bears a direct relation to the branching of the generative filaments. This terminal branching is more profuse in the subgenus *Eulemanea* than in *Sacheria;* consequently there is a continuous ring of spermatangia formed at the "nodes" in the former subgenus, while only scattered patches or sori occur in the latter. In the local plants, the ring of spermatangia is rather irregular as a rule, because the terminations of the generative filaments do not meet those of the adjacent structural unit evenly. At maturity, the prominent spermatangial ring is easily identified by its lighter color as contrasted with the carpogonial region, but this difference disappears after fertilization has occurred.

The spermatangia in *Lemanea* possess a distinct but rather elastic thin wall. The cytoplasm is colored greenish-blue, but no distinct chromatophores are present as in the mother-cell which produces them (fig. 20). Each spermatangium may bear more than one spermatium in succession, as shown in figures 21a, b and c. These drawings were made from living material; fixed spermatia invariably undergo pronounced shrinkage and yield poor preparations. The figures just cited show that the spermatia are budded off from the spermatangia as protuberances surrounded by an elastic wall. Prior to liberation there is a contraction of the cytoplasm of the spermatium which frees it from the spermatangial cytoplasm; this may be seen in figures 20 and 21c.

The spermatia seem to have no distinct wall at the time that they are freed from the spermatangium. Plasmolysis and staining techniques consistently fail to demonstrate such a structure in the spermatia of *Lemanea* at this stage of their development, but there can be no doubt that such a wall develops by the time that the spermatium has attached itself to the trichogyne. Figures 6, 7 and 25 to 27 illustrate the walled condition of spermatia when they are attached to the trichogyne. Upon liberation, the spermatium leaves behind it the empty walls of the spermatangium. These

FIGS. 24–34. Camera lucida drawings of *Lemanea australis.* FIG. 24. Surface view of trichogyne with attached spermatium. × 410. FIG. 25. Spermatial nucleus migrating to the carpogonium through the trichogyne; supernumerary male nuclei in various stages of disintegration. × 825. FIG. 26. Fusion of male and female nuclei (carpogonium cut off from trichogyne); note divided male nucleus. × 825. FIG. 27. Spermatial nucleus below egg nucleus, and in early prophase, just prior to fusion. × 825. FIG. 28. Ten male chromosomes surrounding the female nucleus. × 900. FIG. 29. First division of the zygote nucleus; note two nurse cells. × 825. FIG. 30. Early gonimoblast initials. × 825. FIG. 31. Further development of gonimoblast with sterile lateral cells intact. × 825. FIG. 32. Sectional view of young cystocarp showing marked differences in nucleolar size of the various cells as well as cytoplasmic variability. × 825. FIG. 33. Sectional view of older cystocarp at beginning of the nuclear migration; note three nurse cells. × 410. FIG. 34. Detail of nuclear and cytoplasmic migration to form placental cell of the cystocarp; note ruptured pit-connections. × 600.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empty ruptured walls give the appearance of hairs over the nodal region in living preparations observed at low magnification. The cytoplasm of living spermatia is slightly pigmented with a bluish-green color. Both Feulgen- and haematoxylin-stained nuclei appear to be in late prophase at the time of liberation, a condition which seems to be universally true for Floridean spermatia when they are shed from the spermatangia.

The female organs. While the spermatangia are confined to the "nodes" and immediately adjacent portion of the "internode," the carpogonial branches are restricted to the "internode" of the sexual shoot. They arise as lateral branches from the cells of generative filaments which are peripherally arranged just within the cortical cells of the thallus (figs. 22 & 23). In the present species the carpogonial branches tend to be more densely aggregated on those portions of the generative filaments which coincide with their point of origin from the cruciate ray cells, i.e. in the center of the "internode." The length of the carpogonial branches is proportional to the distance from the medullary cells of the cortex to the generative filaments on which they are borne. Consequently, the carpogonial branch may consist of from four to ten ovoid cells, but six cells is the most common number. This variability in the length of the carpogonial branch is in sharp contrast to the situation in the higher Florideae, where the number of cells is quite constant. Fritsch (1945a) notes that the cells of carpogonial branches are commonly colorless in most of the Rhodophyceae. This is not the case with the immature carpogonial branch of *Lemanea*.

Plastid formation can be clearly followed in the developing carpogonial branches. The details of this process will be described subsequently, but they indicate that the carpogonial branch is probably a modified vegetative branch of the thallus. Figure 22 is a drawing of a young carpogonial branch in the living condition. Diffuse pigment in the younger distal cells becomes progressively localized and aggregated into definite plastids in older cells in the living branch. Plastids in the older basal cells are usually composed of reticulated segments; pyrenoids do not occur in *Lemanea*.

As the carpogonial branch matures, two obvious changes occur: the plastids gradually disintegrate, especially in the carpogonium (fig. 23), and there is a profuse development of almost spherical-celled branches from all the cells of the carpogonial branch except the carpogonium itself. These changes occur prior to fertilization (fig. 23).

The carpogonium is borne on the apex of the carpogonial branch; it penetrates to the exterior of the thallus by the extension of its trichogyne, which pushes between the cells that lie in its path (fig. 22). Sirodot (1872) found it impossible to ascertain whether or not more than one cell of the carpogonial branch might function as a carpogonium. This difficulty was due chiefly to the presence of the sterile branches to which reference has

just been made. These branches are partially surrounded by the vegetative cells of the cortex, and, therefore, further developmental processes are largely obscured in living, unsectioned plants. Inspection of sectioned and stained material leaves no doubt that each carpogonial branch gives rise to a single carpogonium. Carpogonia may be so close together that their lateral sterile branches intertwine; thus the mistaken impression arises that two carpogonia are borne on a single large carpogonial branch.

The carpogonia of all Florideae have a more or less conspicuous trichogyne, a prolonged process with which the spermatia make contact. In *Lemanea* the trichogyne is generally bifurcated, and its distal extremities may lie directly upon the pseudo-parenchymatous cells of the outer cortex, or may extend some distance above them. Figures 5 to 7 and 23 to 27 show the diverse forms that the trichogyne may assume. No evidence of a nucleus in the trichogyne has been found at any stage of its development. Its cytoplasm at maturity is faintly bluish-green in color with no localized pigmentation or plastids. Just prior to fertilization, the trichogyne secretes a mucilaginous covering which extends down to the apex of the carpogonium proper.

There is a single nucleus in the broad base of the carpogonium; this is surrounded by cytoplasm which is denser and more heavily pigmented than that of the trichogyne, but at the time of fertilization there is no longer any evidence of the primordial plastids that can be seen in earlier stages. The nucleus is at interphase, and, just before fertilization it moves up from its usual position near the base of the carpogonium to the neck region, as shown in figure 5.

Fertilization. The young sexual shoots, which were initiated upon the chantransial filaments in the preceding December, reach sexual maturity by the middle of February. Inasmuch as growth is apical, one can observe a series of stages on a single sexual shoot leading from the initiation of the spermatangial and carpogonial regions, through fertilization and post-fertilization stages. This seriation persists for a considerable period, due to continued apical growth. The large number of spermatia produced, the alternating zones of spermatangia and carpogonial branches, together with the close promixity of the sexual shoots apparently enhance the incidence of fertilization, despite the fact that the plants inhabit turbulent waters. They are, in fact, ready for fertilization at the very time when the streams are most disturbed, i.e. in the late winter and early spring. The thick mucilaginous wall of the trichogyne is a further adaptation which increases the chances for sexual union. In addition, penetration of the surface of the thallus by the trichogyne apparently makes available a gelatinous surface deposit in that local region, as is evidenced by the accumulation there of bacteria, unicellular algae and other debris.

When a spermatium lodges against the trichogyne an open connection is soon established between the two structures. Figure 24 shows a surface view of this connection in a living specimen. At the same time, the single prophase nucleus completes its division, as is evident from figures 7 and 25 to 27. Eventually all the contents of the spermatium may flow into the trichogyne, so that only the empty spermatial wall remains attached to the arm of the trichogyne; this is clear from figure 6.

Only one male nucleus enters into the carpogonium proper, although both may enter the trichogyne (figs. 25 to 27). No cases of polyspermy have been observed. While passing down the trichogyne into the carpogonium, the male nucleus appears to be in interphase. Since many spermatia may become attached to the trichogyne and empty their contents into it, there are usually several disintegrating nuclei to be observed in the trichogyne during the passage of the functional male nucleus to the carpogonium, as illustrated in figures 25 to 27.

After the male nucleus has migrated to the region of the egg nucleus, the trichogyne becomes abstricted from the base of the carpogonium (figs. 8 and 26 to 28). The trichogyne and any disintegrating supernumerary spermatial nuclei wither away; a radial protuberance of the carpogonium, that portion originally connected to the trichogyne, persists until much later in development; cytoplasmic disorganization initiates this disintegration.

The egg nucleus is considerably larger than the male nucleus, but the latter enlarges somewhat before actual union. Both unite near the base of the carpogonium. Figure 8 shows the male nucleus just above the egg nucleus at the time of union, while figures 26 and 27 illustrate two successive stages in that process. In figure 28 it is evident that the spermatial nucleus probably initiates union, for the egg nucleus is still in the interphase condition, while the spermatial chromosomes are already fully formed.

The zygote is readily distinguishable from the underlying hypogynous cell and its many sterile companion cells by the large size of its nucleus and nucleolus and particularly in its dense cytoplasm. This difference in structure is apparent in figure 29. The zygote and its nucleus increase in size soon after fertilization.

Cystocarp formation. In tetraspore-forming Florideae the first nuclear divisions of the zygote are not meiotic. While *Lemanea* does not form tetraspores, no conclusive evidence of meiosis has been found in the fertilized carpogonium, although hundreds of specimens have been studied.

(*To be concluded in the next issue*)

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BIBLIOGRAPHIC NOTES ON PALISOT DE BEAUVOIS' PRODROME

HOWARD A. CRUM

The *Prodrome des cinquième et sixième familles de l'aethéogamie* by Palisot de Beauvois (1805) ranks high among the early taxonomic treatments of both mosses and lycopods; because it appeared so near the starting date for bryological nomenclature, it is particularly important to bryologists. Seventy-one new species, four new varieties and many new combinations occur in the "Table des Mousses," which is an index to all the species of mosses known to Palisot de Beauvois. Descriptions of 42 genera, 10 of which appear to be new, are found in an introduction to the "Table des Mousses." Several editions of the *Prodrome* or of parts of it were published; the introductory portion of the edition of 1805, including the descriptions of all the genera except *Rhacopilum*, was reprinted from the *Magasin encyclopédique* (1804). In other words, nine of Palisot de Beauvois' genera date from 1804 rather than from 1805. Palisot de Beauvois made no mention of his earlier publication of these genera, and, so far as I know, no bryologist subsequent to his time has taken cognizance of it.

After the generic descriptions, the members of each genus are listed under the names assigned them by previous authors. With two exceptions, they were not listed as new combinations until 1805 when the "Table des Mousses" was added. In 1804 the combination *Hedwigia ciliata* was attributed to Hedwig and to Bridel, but neither author published such a combination, and, consequently, regardless of intent, Palisot de Beauvois should be considered its author. *Hedwigia ciliata* was relegated to the synonymy of *H. diaphana* in the "Table des Mousses" in 1805, and, therefore, the customary citation of the *Prodrome* (1805) as the origin of the name is quite incorrect. Also in 1804, Palisot de Beauvois changed the specific epithet of *Anictangium bulbosum* Hedw. to *pteridioides* because Hedwig had misinterpreted a portion of a creeping stem at the base of the single branch in his specimen as a bulbous base. Hedwig's specific epithet, however inappropriate, clearly takes nomenclatural precedence over that suggested by Palisot de Beauvois.

Necessary changes in nomenclatural "bookkeeping" are summarized below. The original spellings, some of them obvious barbarisms, have been retained.

Hedwigia ciliata (Hedw.) Beauv. Mag. Encyc. 5: 304. 1804.

Lasia Beauv. Mag. Encyc. 5: 315. 1804, non Lour. 1790.
Streblotrichum Beauv. Mag. Encyc. 5: 317. 1804.
Cicclidotus Beauv. Mag. Encyc. 5: 319. 1804.
Hymenopogum Beauv. Mag. Encyc. 5: 319. 1804.
Orthopixis Beauv. Mag. Encyc. 5: 322. 1804.
Amblyodum Beauv. Mag. Encyc. 5: 323. 1804.
Cyathophorum Beauv. Mag. Encyc. 5: 324. 1804.
C. pteridioides Beauv. Mag. Encyc. 5: 324. 1804.
Pilotrichum Beauv. Mag. Encyc. 5: 327. 1804, non Hook. f. & Anders. 1872.
Pogonatum Beauv. Mag. Encyc. 5: 329. 1804.

The introductory essay on the families and genera of mosses also appeared in 1806 as an English translation in Konig and Sims' *Annals of Botany*, and, posthumously in 1822, a revised French edition in the *Mémoires de la Société Linnéenne de Paris* added five genera (*Trematodon* Michx., *Codrioporus* Beauv., *Leskea* Hedw., *Climacium* Web. & Mohr and *Timmia* Hedw.), as well as several illustrations and various discussions of generic concepts. *Catharinaea* Ehrh. and *Diphyscium* Mohr replaced *Atrichum* Beauv. and *Hymenopogum* Beauv., respectively; *Cynontodium* Hedw. was abandoned.

It is not generally known in America that Palisot de Beauvois, a Frenchman, lived in Philadelphia between the years 1792 and 1798 and collected extensively from New York to Ohio and south to Georgia. About one-third of the mosses described in 1805 were collected in North America. He had also lived and collected in Haiti for three years previous to his sojourn in the United States; his Haitian collection of mosses were apparently lost, however, along with his other collections either by piracy in the Caribbean or by shipwreck on the North Atlantic. No Haitian mosses are included in the *Prodrome*. Merrill (1936) wrote an account of Palisot de Beauvois' life as a botanical explorer in Africa, a political refugee from Haiti and an emigré forbidden to return to revolutionary France for many years because of his aristocratic birth. For further details of Palisot de Beauvois' life and botanical career, reference is made to Merrill's interesting and informative article.

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————. 1806. Continuation of the aetheogamia. The Lycopodia. Ann. Bot. Konig & Sims **2**: 244–251.

————. 1822. Muscologie, ou traité sur les mousses. Mém. Soc. Linn. Paris 1: 388–472. *pl. 1–11.* (Reprint, pp. 1–88. *pl. 1–11.* D'Hautel. Paris.)

Merrill, E. D. 1936. Palisot de Beauvois as an overlooked American botanist. Proc. Am. Philos. Soc. **76**: 899–920.

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TORREYA

BOOK REVIEWS

Flora de Cuba, Volume II. By Hermano Leon (J. S. Sauget) and Hermano Alain (E. E. Liogier). Contribuciones Ocasionales del Museo de Historia Natural de La Salle, 10. 456 pages. Frontispiece and illustrations 1–171. Paper covers. Colegio de La Salle, Havana, Cuba. 1951. $5.50.

The second volume of Brother Leon's Flora de Cuba continued the contribution of this able botanist to the knowledge of the vegetation of that island. In this volume he is assisted by Brother Alain.

The pattern established in volume one has been followed in Volume II. Brief but adequate descriptions, in Spanish, of series, orders, families, genera and species as represented in Cuba are given. Emphasis is placed on the species occurring in Havana province and these are handled with complete analytical keys. Other species found in Cuba but not occurring in Havana province are given synoptical grouping. The principal synonyms are supplied for the species treated but bibliographic references which would be useful for each species have been omitted. Collections are cited only when the species is known from a single collection and those cited are principally Wright's material.

A key to the orders of the Choripetalae is supplied at the beginning of the book but the text itself covers only the Casurinales through the family Meliaceae of the Geraniales. Family keys are supplied with the treatment of each order and generic keys are complete for each family. Unfortunately page references to the locations of orders and families in the text are not given in the key to the orders. While an index is to be found for the volume it will be necessary to refer to Volume II for the key to some of the families to be treated in Volume III.

The Cuban botanists Roig and Acuna have prepared the treatments of the genus Ficus and the families Phytolacaceae, Lauraceae, Simarubaceae and Meliaceae. The treatments of the genera Peperomia and Coccoloba have been adapted from the monographs of Yuncker and Howard respectively. A bibliography lists the principal monographic studies of the families and genera treated in Volume II and will be useful to the student of the Cuban flora.

Volume II of the Flora de Cuba is well illustrated with habit photographs, photographs of herbarium specimens and line drawings. Indices of the illustrations, scientific names and common names, the latter mostly Spanish, have been supplied. A tabular summary of the number of genera and species treated in the volume is given. An appendix of three species, all foreign to Havana province, on page 420 is apt to be overlooked.

In general the family treatments are conservative, for example, the many segregate genera of the Leguminosae proposed in the North American Flora and used in Britton and Wilson's Flora of Puerto Rico have not been accepted. The only inconsistency in the book is the adoption of the Spanish spelling of the family name while the spelling of all scientific names is the conventional latin.

Leon and Alain are to be commended for this, the second of the proposed five volumes treating the flora of Cuba. Brother Alain has been awarded a Guggenheim fellowship to allow him to study the Cuban collections in American herbaria during the summers. His careful analysis of the many species described by Britton, Wilson, Ekman and Urban makes the Flora de Cuba a significant contribution to Antillean botany.—RICHARD A. HOWARD, Harvard University.

Texas Range Grasses. By Benjamin Carroll Tharp. xiv + 125 pages. Illustrated. The University of Texas Press. 1952. $4.00.

Our first inclination was to return this book or content ourselves with a note about it. Of the large number of grass species native to Texas only 168 are included. A review of such a book might be more appropriate in a farm, or rancher's, journal. No one will deny this. But, on the other hand, it is designed as a basic text in a grass research project and our readers outside of Texas may have such projects in mind. Further, it serves as a brief guide to "vegetational regions of Texas" of which 18 are recognized and mapped. Other maps show topography, average annual precipitation, "precipitation/evaporation figures for points scattered over the state," and soils.

Each region is then described ecologically and floristically. There is then a list of range grasses of the region, or at least of "those species which from the standpoint of soil cover, grazing, or potential biological importance are clearly more significant in the over-all picture." Some species will occur in several regions. These lists are tabulated and each species is assigned to one of five categories, ranging from "so abundant that it dominates the landscape" to "comparatively rare." In view of the fact that this last column always has by far the greatest number of species, we wonder if the application of the quoted passage above was not sometimes debatable. Always the skeptic, we are the more dubious since no method of sampling or of determining relative abundance is mentioned. We wonder if any were used? We wonder if the guesses were even made with the list in the field, in how many stands for each region?

Several of the species have drawings "for purposes of identification." We hope that those who make the determinations in this project, which are leaned upon for accurate floristic data, will make use of more carefully detailed diagnostic criteria. It seems to us that the artist was not shown the characteristics which differentiate some of the related species. The number of strong veins and the relationship of the various flower parts, for example, are often missing.

There are two appendices and a brief bibliography.

Perhaps the Director of the Plant Research Institute, Dr. W. Gordon Whaley, has reviewed the book better than we have when he states: "The most critical element in progress is the initiation of the action. This publication represents an element in the initiation of our fundamental research related to some of the grassland problems."—JOHN A. SMALL, New Jersey College for Women, Rutgers, The State University of New Jersey.

Vegetation and Flora of the Sonoran Desert. By Forrest Shreve and Ira L. Wiggins. **Vol. I. Vegetation of the Sonoran Desert.** By Forrest Shreve. xii + 192 pp. + 37 full page plates. Carnegie Institution of Washington Publication 591. Washington, D. C. 1951. Paper bound $3.25; cloth $3.75.

"Forrest Shreve dedicated virtually his entire scientific career to the study of the botanical features of the arid regions of North America." He was thirty-six years at the Desert Laboratory of the Carnegie Institution of Washington at Tucson, Arizona, and after retirement in 1945 he continued the studies until his death in 1950. The original plan was to cover the Sonoran, Mojave, Chihuahuan, and the Great Basin Deserts in successive studies, perhaps culminating in a comprehensive treatise of the North American Desert in its entirety. Considerable field work was done in the four deserts but only that in the Sonoran was completed. It is to be hoped that someone may have access to the data and complete the other studies. Professor Wiggins' floristic work will constitute volume II of this publication and Professor Ivan Johnston has already published (Jour. Arnold Arboretum) some floristic work in the Chihuahuan Desert.

The boundaries of the Sonoran Desert are similar to those established by earlier authors except for inevitable refinements brought out by this longer study based on "the Sonoran Desert . . . as a region of biological unity." Chapter 2 deals with physical features of the Sonoran Desert. Chapter 3 is practically a treatise in itself. A single page gives an extraordinarily concise and penetrating statement of the general characteristics

of deserts. Types of plants, species of plants, and communities of plants are then treated in that order. It becomes apparent that ecological principles such as "succession" and "climax" are also modified by desert conditions. The four parts of the North American Desert (to most of us the four North American Deserts, Chihuahuan, Great Basin, Mojave, and Sonoran, are briefly described and contrasted. Thereafter the author limits himself to the vegetational aspects of the Sonoran Desert.

The size of the Sonoran Desert, some 120,000 square miles, dictated that a study of its ecology as a whole be general and descriptive rather than precise and statistical. The height, density, simplicity of composition, and physiographic control of vegetation are discussed; also the consistency of local distribution and the subordinate plants. In considering life forms, Shreve recognized twenty-five. The characteristics of each, examples, and their place in the desert picture are stated.

We habitually use geographic terms, names of floristic dominants, or vegetational designations in expressing the character and organization of plant communities. Shreve points out that these three standpoints of designation "are distinct in their rational basis even though their outlines happen to coincide to a greater or less extent." He continues, "It is obvious that the geographic subdivision relates largely to the environmental conditions, which are not a part of the plant life. Floristic and vegetational subdivisions must be made on the basis of their own intrinsic data. The physical setting is a controlling agent with reference to the vegetation, but is not one of its characteristics. The custom of using the habitat as part of the characterization of a plant community is an illogical procedure of long standing."

The Sonoran Desert is broken into seven subdivisions each designated in the three ways just described. Seventy-nine pages are then devoted to the perennial vegetation of these subdivisions. Abundant lists of plants from various communities of each subdivision are included.

Although ephemerals "form about half the flora and also play a conspicuous role in the vegetation in their appropriate seasons" they are treated separately in Chapter 4. Winter ephemerals and summer ephemerals are recognized and again lists are generously provided.

The final chapter deals with "ecological features of characteristic species." Twenty-seven species are discussed in alphabetical order. Thirteen of these are accompanied by maps showing their distribution over the Sonoran Desert while eleven additional species receive the map treatment without comment. Literature citations are brought together locally throughout the book. A list of twenty-seven rather general papers appears at the end. Thirty-seven plates of halftone reproduction of photographs give one a nice visualization of plants, vegetation, and what passes for soil.

The book is a must for ecologists and for reading lists in plant geography. Anyone having a vocational or avocational interest in ecology would find this book a delightful companion while visiting the Sonoran Desert. May we reiterate the plea that the desert studies be completed as originally outlined.—JOHN A. SMALL.

Illustrated Guide to Trees and Shrubs. By Arthur Harmount Graves. x + 240 pages; figs. 1–116; plates 1–45. Published by the author, Wallingford, Conn. 1952. $4.00.

This book sets out to include all woody plants, whatever their growth habit, commonly found in the Northeastern States, either in the wild or cultivated areas. There are now a goodly number of treatises embodying this ambition to a greater or less extent. Indeed this "book is in large part an illustrated edition of the Teaching Guide to Trees and Shrubs of Greater New York" originally prepared by Graves and Hester M. Rusk at the Brooklyn Botanic Garden. It is considerable of an expansion however.

Such books may be separated into two groups on the basis of what they aim to do. One group is just a key or series of keys and when one works his way to the name of the plant that is all he has to show for his pains. The author introduces one and walks away. What awkward situations sometimes develop under such circumstances! The books in the

other group are more considerate. One is led through the keys or by the keys to the name of the plant and then told something about its characteristics, its distribution, its ecology, and its relatives. Graves' book is from the latter group. We found it to be efficient and interesting. Those plants tried in summer keyed out rapidly and with a minimum of "tight" decisions to make. A colleague, using twigs in winter, did not find the going so easy. Most keys, before they get done with it, expect one to have buds, leaves, flowers, fruit, and nature of the juices exuded. This book is rather good about showing one how to make do without the ready availability of a character that is called for. For instance, juice milky or otherwise may be determined by cutting a bod if the plant is not in leaf.

The keys are multiple choice. Sometimes there are four possible choices. Each choice is indicated by a capital letter in boldface in the main key but these are omitted in the keys under genera. One difficulty is that the next step after any letter is the next letter of the alphabet, no matter how many times that letter has been used before. Since the various choices are sometimes a page or more apart be sure to read the "(3rd C, p. 18)" because some letters are used over several times and it is not impossible to miss a counter-choice and end up in an impossible situation. For instance, on page 17 we have "C. Lvs. parallel veined" and "C. Lvs. palmately veined (3rd C, p. 18)" but if we hurry on too fast to locate our plant with the pinnately veined leaves we may pick up the third C on p. 19. This is disastrous because that C is under a different B. It is rewarding to read carefully.

An altogether different key at the back of the book holds out "short cuts to naming" that are often helpful in the way indicated. Owners of the book should familiarize themselves with these possibilities.

The body of the book is interesting. There is always the problem of where does the author draw the line? What does he really include, what does he exclude? Graves does not always stick to his stated limits. One can find information about palms in general; about *Sequoia* and *Metasequoia* in particular. One can find *Phoradendron* and *Arceuthobium*. The only complete omission that we noted was *Hudsonia* (and *Lechea*?). Graves is surely not a splitter. He has only five blueberries. Six roses serve his purpose and the impatient are quieted with the statement, "over 5000 vars. having been named." There is no dodging of issues though. Seven species of *Rubus* will key out and we thought *Crataegus* disposed of nicely by the statement, "They can be identified as Hawthorns" plus the understatement, "several native spp. grow in our area, but they are difficult to distinguish without fls. and frs." We like this recognition of the fact that, for the purposes of this book, sometimes identification to the genus or a few of the species is enough. Where lengthy technical descriptions are required for differentiation Graves states, "these can be found in the manuals." At that point shall we say one no longer needs a Guide?

The drawings by Maud Purdy are excellent and will often help one to determine his woody plant or to be confident that his determination is correct. A glossary, "some helpful references" (including the manuals), and an index conclude the book.

—JOHN A. SMALL.

FIELD TRIP REPORTS

April 26. Harriman Section, Palisades Interstate Park, N. Y. This trip brought in a list of about 60 species of seed plants, mosses, ferns, and lichens. Of particular interest was the abundance of dwarf ginseng at Lake Tiorati and at Lake Nawahunta, an extensive stand of Phragamites on the floor of a drained beaver pond, revisiting a stand of *Isoetes engelmanni* near an inlet to Tiorati, and an unusually dense stand of *Andrea petrophila* on a steep granite rock face near the latter lake. Attendance 3. Leader: Lee A. Ellison.

May 3. Hacklebarney State Park, N. J. The dwarf ginseng was abundant here as at Tiorati but in addition a spectacular number of *Orchis spectabilis* were seen in three or four stands. The similarity of this terrain with that visited the previous week was noted. A few additional spring flowers were noted in bloom. One of the few locally known stands of the hepatic, *Metzgeria furcata*, was visited and found to be increasing slowly in its extent. Attendance 9. Leader: Lee A. Ellison.

NOTE

Dr. David F. Marsh, formerly head of pharmacology at West Virginia University, School of Medicine, is now Executive Vice President of the Transandino Company of Palo Alto, Calif. The research work of both Dr. Marsh and Transandino on the pharmacology and processing of curare is well known in this country and abroad.

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INDEX TO AMERICAN BOTANICAL LITERATURE

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LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

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